NATURAL MORTALITY AND MOVEMENT OF JUVENILE COD (Gadus SPP.) INHABITING EELGRASS (Zostera marina) IN COASTAL NEWFOUNDLAND WATERS

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NATURAL MORTALITY AND MOVEMENT OF JUVENILE COD (*Gadus* spp.) INHABITING EELGRASS (*Zostera marina*) IN COASTAL NEWFOUNDLAND WATERS

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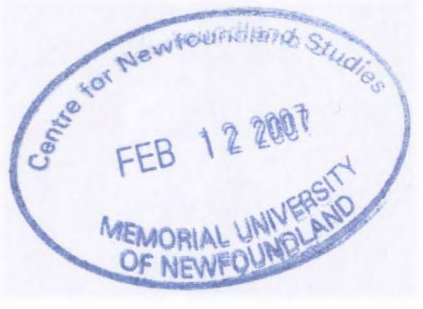

Abstract

The natural mortality of teleost populations is age-dependent - young, small-bodied individuals experience comparatively higher mortality rates than older, larger individuals. The use of structurally complex habitat, such as eelgrass (*Zostera marina*) and macroalgae, is believed to increase survival of early stages by providing protective cover from predators and increased food availability. However, few studies have actually quantified natural mortality rates for juvenile cod associated with nearshore habitat. I determined mortality rates for juvenile Greenland cod (*Gadus ogac*) and Atlantic cod (*G. morhua)* associated with eelgrass in the coastal zone of Newman Sound, Newfoundland. During Oct-Nov 2002, I fin-clipped 818 age-0 Greenland cod; an additional 1442 age-1 Atlantic cod were fin-clipped during June-July 2003. During Oct-Nov 2003, a further 765 age-0 Greenland cod were individually marked with visible implant alphanumeric (VIalpha^{TM}) tags. Re-sampling revealed that juvenile cod remained near the site of release, rarely venturing beyond a distance of a few hundred metres. For age-1 Atlantic cod in eelgrass habitat, the mortality rate was $M = 0.068day^{-1}$ (estimated using the Jolly-Seber method), which was significantly higher than that predicted ($M = 0.010day^{-1}$) using an age-dependent mortality model based on published cod mortality rates. High mortality rates may be attributed to high predation and other biotic and abiotic sources of mortality (i.e., starvation, environmental extremes). Juvenile cod mortality rates were high despite the availability of areas with complex structure; however, consistently low cod abundances in structurally simple habitats suggest such areas may be too risky to frequent for extended periods.

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Chapter 1: Introduction and Overview

1.1 Natural mortality of juvenile cod

The natural mortality of many teleost populations is stage- and size-dependent, with early, smaller stages experiencing substantially higher rates than older, larger stages (Peterson and Wroblewski 1984). Mortality rates observed during the egg and larval stages can be entirely attributed to endogenous factors, such as lethal genetic or developmental abnormalities, and exogenous factors that include food shortages, predation, disease, parasitism, toxins, environmental extremes, and physiological stress (Heath 1992). Susceptibility to density-independent mortality lessens as fish grow. Larger individuals experience increased resistance to starvation, decreased vulnerability to predators, and increased tolerance to environmental fluctuations ("bigger is better" hypothesis; see review by Sogard 1997). The probability of surviving to maturity is positively correlated with individual growth rates. Fast growth rates are thought to allow individuals to reach size refuges from potential predators quicker than low rates (stage duration hypothesis; Houde 1987; cf. Pepin 1991).

Gadids, such as Atlantic cod (*Gadus morhua*) and Greenland cod (*G. ogac*), have evolved life history strategies whereby large numbers of eggs are produced, increasing the likelihood that at least some offspring will reach reproductive age. The probability of reaching maturity is low for northern cod with approximately one individual in a million surviving to the age of 3 years (Hutchings 1999). Numerous quantitative estimates of natural mortality rates have been reported for the egg (Fossum 1988; Campana et al. 1989; Heessen

and Rijnsdorp 1989; Kristiansen et al. 1997; Serchuk et al. 1994; Wieland et al. 2000) and larval (Fossum 1988; Blom et al. 1994; Kristiansen et al. 1997) stages; however, few studies exist that document estimates for juveniles (Kristiansen et al. 2000a), particularly those aged 0-1 years. Knowledge of mortality rates during the early life stages of fish populations is fundamental because the survival of young individuals can be used to predict year-class strength and subsequent recruitment to fisheries (Sissenwine 1984; Peterman et al. 1988; Campana et al. 1989). Maximum year-class strength is established during the pelagic egg and larval phase (Myers and Cadigan 1993a; Anderson and Gregory 2000), which is then succeeded by density-dependent regulation during the demersal juvenile stages prior to recruitment (Myers and Cadigan 1993b; Anderson and Gregory 2000). The majority of mortality estimates for post-settled juvenile cod result from stock enhancement studies conducted in Norway (Svasand and Kristiansen 1990; Ottera et al. 1999; Skreslet et al. 1999; Kristiansen et al. 2000a,b; Julliard et al. 2001; Larsen and Pedersen 2002). However, these estimates should be used with caution because reared cod may differ from wild cod in terms of behavioural responses to predators, prey, and their environment after release. For example, naive reared cod are less likely to form aggregations than experienced wild cod, making them more prone to predation from certain predators (e.g., shorthorn sculpin *Myoxocephalus scorpius*; Whitehead 2005). Nonetheless, enhancement studies have demonstrated that mortality during the juvenile period is size-dependent and varies with season, geographic location, predator species and density, availability of alternate prey, and food availability. The occurrence of relatively high abundances of age 0-1 cod in shallow

water habitats of Newman Sound, Newfoundland, offered an unique opportunity to determine the natural mortality rates of the juvenile stage. This age-class is not vulnerable to fisheries due to its small body size while the possibility of capture as by-catch is negligibly low because of its nearshore, shallow-water distribution. Therefore, natural mortality (M) estimates are not confounded by fishing mortalities (F), as often is the case with mortality studies of large-bodied fish populations (Ricker 1975).

Many factors may contribute to the natural mortality of juvenile cod; however, the major source of mortality appears to be predation. A wide range of predators consume juvenile cod and include invertebrates, fishes, birds, and mammals (Scott and Scott 1988; see review by Palsson 1994). In Newman Sound, tethering studies have identified the predominant piscine predators as sculpins *Myoxocephalus* spp., white hake *Urophycis tenuis*, Atlantic cod, and Greenland cod (Linehan et al. 2001; Laurel et al. 2003a). Harbour seals *Phoca vitulina*, otter *Lutra lutra*, and minke whale *Balaenoptera acutorostrata* represent potential mammalian predators that are present in the fjord and potential avian predators, such as gulls, terns, mergansers, cormorants, loons, eagles, and osprey, are common (Linehan et al. 2001; personal observation). Nonetheless, the extent of predation by these groups has received little attention. In other areas, there are indications that these groups may have significant impacts on juvenile cod populations. For example, during stock enhancement studies in Masfjorden, Norway, more than 7% of the tags used during one experiment were found amongst regurgitates at the roosts of cormorants *Phalacrocorax carbo* and shags *P. aristotelis* (Ottera et al. 1999). The presence of a large host of potential predators in Newman

Sound may restrict juvenile cod distribution and movement to the shallow nearshore. Linehan et al. (2001) suggested that age-0 cod most frequently inhabit the shallow margins of the coastal environment as a result of lower predation risk compared to deeper waters where larger piscivorous fishes reside. Furthermore, piscine predators, which are typically at least twice the length of their prey (Miller et al. 1988; Bogstad et al. 1994; Salvanes 1995), are thought to be deterred from entering shallow waters by the threat of avian predators (Linehan et al. 2001).

1.2 Juvenile cod movement

The rate and extent of movement by gadids appears to be stage- and size-specific, and may vary depending on species, sexual maturity, diel period, season, and geographic location. Some populations of adult northern Atlantic cod have historically undertaken large-scale seasonal migrations among overwintering, spawning, feeding, and coastal nursery habitats (Templeman and Fleming 1963; Lear and Green 1984). The observed circuit of migration (Harden Jones 1968), which often spans tens to hundreds of kilometres, generally involves a transition from spawning areas in offshore shelf waters during the spring (Lear and Green 1984; Hutchings et al. 1993) to inshore areas in summer to feed on capelin and other nearshore prey (Lilly 1987). The migration is completed when cod return to deep offshore waters in autumn (Templeman 1965; Lilly 1987; Methven and Piatt 1989). Similarly, but at a smaller geographic scale, large juveniles (age 2-4) exhibit seasonal movements, migrating from relatively shallow coastal waters inhabited during spring and summer to deeper waters in late autumn (Cote et al. 2004). Such movements may be mediated by abiotic (e.g.,

temperature, salinity) and(or) biotic (e.g., food availability, predator abundance, cod density) factors; however, it is uncertain whether similar seasonal movements are undertaken by cod aged 0-1 years.

Numerous studies have been devised, typically involving mark-recapture experimentation, to determine the movements of juvenile cod aged 0-1 years. Reported conclusions about movements have been contradictory, with displacements ranging in scale from a few metres to thousands of metres. Post-settled juvenile cod in coastal habitats of St. Mary's Bay, Nova Scotia, have been described as extremely territorial and exhibiting high site fidelity (Tupper and Boutilier 1995a,b). In contrast, age-0 cod that inhabit nearshore Newfoundland waters appear to be more mobile (Laurel et al. 2004). Newly recruited demersal age-0 cod in Trinity Bay were observed to remain localized, restricting movements to a few hundred metres in the shallow coastal zone (Grant and Brown 1998), but important (i.e., high-use) habitats were also very localized in that study. In adjacent Bonavista Bay, mark-recapture experimentation and observed density-dependent aggregatory behaviour suggested that the scale of age-0 cod movement was greater, possibly encompassing thousands of metres (Laurel et al. 2004). Laurel et al. (2004) suggested that discrepancies reported for juvenile cod movement among studies may result from the presence of differing habitat and shoreline complexities, unique genetic or phenotypic population characteristics, and(or) differing degrees of habitat heterogeneity. Furthermore, the range of movement for post-settled juvenile cod appears to be size-dependent. Small age-0 individuals have more restricted movement than larger age-1 cod (see Schneider et al. 1999; Methven et al. 2003).

With increasing age, size, and maturity, juvenile cod seem to be less associated with nearshore habitats and begin to exhibit the migratory behaviours of older cod. Pihl and Ulmestrand (1993) observed relatively stationary behaviours for tagged cod <30 cmSL in length during summer and autumn along the Swedish coast; however, over the following winter and spring, larger cod (30-50 cmSL) were recaptured several kilometres from tagging sites, possibly while initiating spawning migration. The contradictory reports of juvenile cod movements in nearshore habitats necessitate the inclusion of a movement study while investigating age-class survival.

1.3 Habitat utilization

Juvenile cod minimize predation risk by using structurally complex habitats as protective cover. Habitat use is dynamic and age-dependent; smaller cod inhabit complex structure in shallow depths, while larger individuals are distributed in deeper waters (Cote et al. 2004). In shallow nearshore waters, age-0 cod utilize vegetative cover, such as seagrass (Gotceitas et al. 1997; Grant and Brown 1998; Linehan et al. 2001; Laurel et al. 2003a,b; Laurel et al. 2004) and macroalgae (Gjosaeter 1987; Keats et al. 1987), that presumably diminish the forage efficiency of larger piscivorous fishes (e.g., Crowder et al. 1992). With increasing body size, juvenile cod become less reliant on vegetative cover as a predator refuge and more frequently inhabit coarse substrates, such as boulder, cobble, and gravel in deeper waters (Lough et al. 1989; Gregory and Anderson 1997). Age-1 cod with mottled colouration frequent gravel, using crypsis to diminish capture probabilities, whereas older juveniles, aged 2-3 years, are more commonly observed using boulder and cobble substrates

for protective cover (Gregory and Anderson 1997).

Though frequently associated with complex structure, juvenile cod also utilize bare habitats in response to changes in the densities of young conspecifics or their potential predators (Laurel et al. 2004). Laboratory studies have demonstrated that the presence or absence of a potential predator influences habitat use by age 0+ cod (Gotceitas et al. 1997). Prior to exposure to an older conspecific, juvenile cod frequent sand and gravel substrates; however, after exposure, highly complex habitats (boulder, eelgrass), which increased latency of time until capture, are utilized more often (Gotceitas et al. 1997). Field studies further show that habitat selection is density-dependent for juvenile cod (Laurel et al. 2004). High cod abundance, and subsequent saturation of eelgrass habitat, has been suggested to force post-settled individuals into non-vegetated areas where behavioural adaptations, such as aggregation, are used to presumably diminish predation risk (Laurel et al. 2004). Occurrence of juvenile cod in structurally simple habitats (i.e., mud, sand) may also be species-specific because Atlantic cod exhibit a lower affinity for complex structure than Greenland cod at small spatial scales ($800m^2$; Laurel et al. 2003a).

1.4 Morphological and ecological differences between juvenile Atlantic cod and Greenland cod

Juvenile Atlantic cod and Greenland cod, aged 0-1 years, co-occur in coastal Newfoundland waters (Methven et al. 2001) at similar lengths and are difficult to distinguish morphologically (Methven and McGowen 1998). Predators appear to prey indiscriminately on juvenile Atlantic and Greenland cod (Laurel et al. 2003), probably because of their inherently similar morphology and behaviour. Nevertheless, the two species may have

different survival probabilities during the juvenile stages based on differences in their life histories. For instance, Atlantic cod typically spawn pelagic eggs in deeper waters off Newfoundland during the spring. Developing eggs and larvae are transported to inshore areas by wind and currents. Atlantic cod settlement occurs in the nearshore during multiple recruitment pulses; the first occurring in August followed by subsequent pulses (Methven and Bajdik 1994; Grant and Brown 1998; Gregory et al. 2002). Little is known of pre-spawning movements of Greenland cod in Newfoundland. However, in Hudson Bay, adults spawn demersal eggs beneath the ice of estuarine waters during March and early April (Mikhail and Welch 1989). In eastern Newfoundland, juvenile Greenland cod settle in a single recruitment pulse in July/August (Laurel et al. 2003b). The differences in the timing of settlement pulses may affect the survival of both species through density-dependent effects. Greenland cod typically recruit to nearshore habitats of Newman Sound earlier in the summer than Atlantic cod. However, the settlement pulse of Greenland cod usually coincides with the recruitment pulse of a third gadid - white hake (Ings 2005). Depending on relative densities, competition for habitat and food may be high amongst these species and may result in higher mortalities for Greenland cod if individuals are forced to occupy areas with suboptimal habitat and food abundances. Because juvenile Atlantic cod arrive after both Greenland cod and white hake have become established in nearshore Newman Sound (Ings 2005), the effects of interspecific competition may be higher for Atlantic cod than Greenland cod (B. Laurel, Memorial University of Newfoundland, personal communication).

1.5 Mark-recapture experimentation

The release of marked individuals and subsequent recapture allows ecologists to determine population identity, movements, abundance, age, growth, mortality, behaviour, and enhancement success (MacFarlane et al. 1990). Numerous mark-recapture techniques have been devised to estimate population size and the components responsible for abundance variability in open populations: recruitment (birth + immigration) and loss (mortality + emigration). Few models permit the determination of all quantities simultaneously (Pollock et al. 1990). During my study, I used the Jolly-Seber method (Jolly 1965; Seber 1965; see comprehensive reviews by Seber 1982; Pollock et al. 1990; Krebs 1999; Pine et al. 2003). After assuming permanent emigration, this approach permits determination of population size at each sampling date (excluding the first and the last), estimation of apparent survival between samplings, and the addition of new recruits, which is part of the recruitment dynamic of the animals in my study. The estimated survival rate is confounded because mortality cannot be distinguished from emigration. True survival rate can be determined if either emigration is negligible or quantifiable (Pollock et al. 1990). Furthermore, the validity of Jolly-Seber estimates cannot be verified unless several explicit assumptions are met. The Jolly-Seber method assumes:

(1) every animal present in the population at sampling time *i* has an equal probability of capture,

(2) survival is equal for every marked animal that is present from one sampling period to the next,

(3) tags or marks are not overlooked or lost, and

(4) all animals are released immediately after the sample and all sample periods have a short duration (Seber 1982).

Assumptions #2 and #3 specifically pertain to the marks applied to released animals; therefore, it is imperative that the marks or tags chosen are appropriate for the species and life stage in question to ensure unbiased estimates of Jolly-Seber parameters. This is particularly true for survival estimates.

Numerous marking techniques have been developed to uniquely identify animal groups and individuals; however, relatively few exist for mark-recapture studies of individuals with small body size (i.e., <100 mmSL). The suitability of available marking techniques decreases further for small individuals, such as juvenile cod, residing in intertidal and subtidal zones where external tags can become tangled in complex structure. One of the most common techniques for marking intertidal fishes is fin-clipping (Moring 1990), the process whereby one or more fins are completely or partially excised (Nielsen 1992). The technique has several advantages (Nielsen 1992):

(1) ease and rapidity of use,

(2) limited growth effect,

(3) suitability for all fishes and invertebrates,

(4) suitability for all sizes and life stages, and

(5) adaptability for short and long term studies.

Ergo, I believe that fin-clipping is an appropriate method for marking young cod in coastal

habitat. Furthermore, unlike external tags, the likelihood of clipped fins impeding the mobility of juvenile cod within nearshore habitats, such as cobble and vegetation, is negligible (Moring 1990). However, the method is not without its drawbacks, which include possible reduced survival, misidentification of marks due to fin regeneration or natural wounds ("false positives"), and negative public opinion (Nielsen 1992; Weitkamp and Sullivan 2002). Furthermore, fin-clipping is a batch mark technique - it does not uniquely identify individual fish - and the number of unique batch marks available is limited by the marking sites; in this case - fins (Nielsen 1992). Prior to mark-recapture studies, particularly those concerned about movement and mortality rates, it is essential to test whether fin-clipping is suitable for the species, body size, and life stage in question.

The soft visible implant alphanumeric (VIalpha™; Northwest Marine Technology, Shaw Island, Washington) tag is a small (1.0x2.5mm), individually coded tag that is injected into the transparent tissue of animals (Rikardsen 2000; Rikardsen et al. 2002). Originally developed as a rigid prototype by Haw et al. (1990), VIalpha tags have been reported to be suitable for mark-recapture studies of various invertebrates (Jerry et al. 2001; Arce et al. 2003; Brown et al. 2003) and fishes (Rikardsen 2000; Griffiths 2002; Rikardsen et al. 2002; Isely et al. 2004), including juvenile Atlantic cod (Olsen et al. 2004). The VIalpha tag is a marking technique suitable for conducting survival, growth, and movement studies where there is a requirement for individually marked animals to be continuously recaptured and released over time (Lebreton et al. 1992) and where it is undesirable to kill specimens in order to individually identify them (Olsen et al. 2004); in contrast with coded wire tags

which require death of the animals. The tags are suitable for marking small individuals though tag retention may be size-dependent with a higher proportion of fish <150 mm experiencing tag loss (27-33%) than larger individuals (4%; Rikardsen 2000). Nevertheless, fish as small as 50 mm have been successfully tagged (Griffiths 2002). VIalpha tags also have little or no effect on survival and growth of marked individuals (Rikardsen 2000; Rikardsen et al. 2002; Isely et al. 2004); however, its use for long term studies (e.g., years) should be cautioned as tags may become obscured with tissue pigmentation with time.

I conducted mark-recapture experiments to determine the natural mortality rates and the extent of coastal movement of age 0-1 cod in Newman Sound, Bonavista Bay. Specifically, I asked (1) are natural mortality rates for juvenile cod low in coastal Newfoundland waters compared to published rates from other areas? and (2) is the movement of juvenile cod inhabiting eelgrass low? To address the first question, I used the Jolly-Seber open population model to quantify the natural mortality of fin-clipped age-0 Greenland cod and age-1 Atlantic cod associated with eelgrass habitat during Fall 2002 and Spring 2003, respectively (Chapter 2). I used modified catch curves to determine natural mortality of age-0 Greenland cod, individually marked with VIalpha tags, during Fall 2003 (Chapter 3). Prior to data collection in the field, I developed a model (Chapter 2) to predict mortality rates for age 0-1 Atlantic cod by regressing published mortality estimates against age. To address the second question, I sampled for marked age-0 Greenland cod (Chapter 2 and 3) and age-1 Atlantic cod (Chapter 2), using beach seine at sites located hundreds of metres along-shore from points of release. Laurel et al. (2004) demonstrated that juvenile cod exhibit density-

dependent habitat use behaviour - juveniles are common over barren habitats during years of high abundance, but only occur in areas of dense cover in years of low overall abundance. If movement rates into unstructured habitats (e.g., mud, sand) are high during high density years because protective structured habitats (e.g., eelgrass) are saturated, then movement rates should be lower during years of low juvenile cod density. My study has important implications for the assessment of year-class strength of inshore cod stocks and the conservation of preferred habitat of juvenile cod in coastal Newfoundland waters.

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Co-authorship statement

Chapter 2: Natural mortality and movement of batch-marked juvenile cod (*Gadus* spp.) in Newman Sound, Newfoundland

G.L. Sheppard designed the research program, organized collection of all data, performed the data analysis, and prepared the manuscript. D.C. Schneider contributed ideas, suggested methods, and advised on statistical analyses. R.S. Gregory contributed ideas, advised on the field program, and assisted in acquiring mark-recapture data. All co-authors contributed to editing of the manuscript.

Chapter 3: Movement, mortality, and growth of individually tagged age-0 Greenland cod (*Gadus ogac*) inhabiting eelgrass in coastal Newfoundland

G.L. Sheppard designed the research program, organized collection of all data, performed the data analysis, and prepared the manuscript. D.C. Schneider contributed ideas, suggested methods, and advised on statistical analyses. R.S. Gregory contributed ideas, advised on the field program, and assisted in acquiring mark-recapture data. All co-authors contributed to editing of the manuscript.

Chapter 2: Natural mortality and movement of batch-marked juvenile cod (*Gadus* spp.) in Newman Sound, Newfoundland

2.1 Introduction

Many teleost fishes experience age- and size-dependent natural mortality rates over their life histories. Mortality is inversely associated with age and body size (Peterson and Wroblewski 1984); egg and larva stages typically exhibit far higher mortality rates than older juveniles and adults. Some species, such as Atlantic cod (*Gadus morhua*) and Greenland cod (*G. ogac*), have evolved life history strategies whereby vast numbers of eggs are produced and released to increase the likelihood that some offspring will reach reproductive age. The probability of reaching maturity is low for northern cod with approximately one individual in a million surviving to the age of 3 years (Hutchings 1999). Numerous quantitative estimates of natural mortality rates have been reported for the egg (Fossum 1988; Campana et al. 1989; Heessen and Rijnsdorp 1989; Kristiansen et al. 1997; Serchuk et al. 1997; Wieland et al. 2000) and larval (Fossum 1988; Blom et al. 1994; Kristiansen et al. 1997) stages; however, few studies provide estimates for young juveniles, aged 0-1 years. Survival during this stage is frequently argued as a good indicator of year-class strength and subsequent recruitment to existing fisheries (Peterman et al. 1988; Campana et al. 1989).

Species that exhibit age- and size-dependent mortality may increase survival by utilizing protected habitats. Koenig and Coleman (1998) observed that survival in juvenile gags (*Mycteroperca microlepis*) was approximately 100% when associated with seagrass habitat. Juvenile cod have also utilize nearshore habitats, such as eelgrass (*Zostera marina*),

kelp, and cobble, to increase survival by reducing predation risk (Keats et al. 1987; Gotceitas et al. 1995; Gotceitas et al. 1997; Gregory and Anderson 1997; Grant and Brown 1998; Linehan et al. 2001; Laurel et al. 2003 a,b; Laurel et al. 2004). Nearshore nursery habitats are thought to increase juvenile cod survival; however, actual mortality rates within habitats such as eelgrass have yet to be determined.

Movement, including directed migration, can bias mortality rate estimates. Animals that disappear may have merely vacated the study area, resulting in underestimation of survival. The movement rates of cod exceed mortality rates at fine scales (<1000 m, <100 d) whereas the opposite was true at coarser scales (Schneider et al. 1999). Older juvenile and adult northern cod undergo large scale seasonal migrations, moving inshore in the spring to summer feeding areas and returning offshore to over-wintering and spawning grounds during the autumn (Templeman 1965; Lear 1984; Rose 1993). Similar migrations to offshore regions are not undertaken by juveniles, aged 0-2 years (Anderson and Gregory 2000), which are affiliated with preferred substrate habitat and inshore nursery grounds. Movements of juvenile cod are less extensive than that of older conspecifics; however, estimates of the extent differ. Age-0 cod in coastal Nova Scotia exhibit high site fidelity (Tupper and Boutilier 1995), whereas studies in coastal Newfoundland (Grant and Brown 1998; Laurel et al. 2004) found that juvenile cod form schooling or shoaling aggregations with little evidence of site fidelity. The geographic variability of movements in coastal waters necessitate that movement be considered when estimating juvenile cod mortality.

Mark-recapture techniques can be used to determine the mortalities, movements, and

population dynamics of animals in both closed and open natural systems. The Jolly-Seber method (Jolly 1965; Seber 1965) has been employed to describe the population dynamics of invertebrates (Fitz and Wiegert 1992), mammals (Johannesen and Ims 1996); birds (Sydeman et al. 1998), reptiles (Kazmater et al. 2001; Tucker et al. 2001), fish (Cone et al. 1988; Koenig and Coleman 1998; Zehfuss et al. 1999; Mills et al. 2002), and British taxicabs (*Yellowus taxii*; Carothers 1973). The Jolly-Seber method was designed for open populations whereby abundance is dynamic as a result of births, deaths, and migration (Krebs 1999). This method is ideal for studies of juvenile fish in marine systems where populations may fluctuate dramatically over short time periods (i.e., days) because mortality and movement rates are high and recruitment to nearshore habitats is occurring.

In nearshore Newfoundland waters, the risk of juvenile cod mortality is lower in shallow depths vegetated by eelgrass than in deeper water with no eelgrass or macroalgae (Linehan et al., 2001). Based on this result I predicted that mortality of juvenile cod in the coastal zone would be low relative to that expected based on cod age. In order to evaluate whether juvenile cod mortality is low in vegetated nearshore habitats of Newman Sound, Newfoundland, I developed an age-dependent survival model using published estimates to determine expected mortality rates for age-0 Greenland cod and age-1 Atlantic cod. Once expected mortality rates were determined, I used mark-recapture methodology and the Jolly-Seber open-population model to infer the natural mortality and movement rates of juvenile Atlantic and Greenland cod that inhabit coastal waters of Newman Sound. The assumptions associated with the Jolly-Seber model were tested to validate mortality rates observed in the

field. Prior to field studies, I conducted an acute mortality assessment to estimate the mortality associated with the batch marking techniques of fin-clipping and fluorescent grit-marking. The results of my study have important implications for the assessment of year-class strength of inshore cod stocks and the conservation of preferred habitat of juvenile cod in coastal Newfoundland waters.

2.2 Methods

2.2.1 Age-dependent mortality model

Prior to field studies, I conducted a literature review to summarize natural mortality (M) estimates for cod eggs, larvae, juveniles (ages 0-4), and adults (age 5+). Though survival may vary with time, mortality rates were assumed to be constant over the duration of each life stage, which allowed yearly M values to be converted to daily M estimates simply by dividing by 365. Mortality estimates for all life stages were plotted against cod age in days. Reported ages were sometimes approximated based on length, a practice typically necessary for juveniles and adults. For example, a cod reported as age-1 could have a daily age ranging from 365 days old to 729 days old. To address this problem, the age in days for juveniles and adult cod were standardized as daily age = 365(yearly age + 0.5). Mortality as a function of age was estimated for each life stage (eggs, larvae, juvenile ages 0-4, and adults age 5+) using a generalized linear model routine with log link and gamma distribution in SAS (1988). Tolerance of Type I error was set at α=0.05 and residuals were examined for homogeneity, normality, and independence. The linear equation determined for the juvenile stage was used to calculate an expected M for juvenile Greenland cod and Atlantic cod of approximately 180

(6 mo) and 425 (14 mo) days old, respectively. No estimates of Greenland cod M could be found in the literature so species-specific M exponential decay plots could not be generated. Use of the Atlantic cod age-dependent mortality relationship for juvenile Greenland cod can be justified because of similarities in habitat choice, prey preference, and availability of potential predators. However, predicted mortality rates may be overestimated for age-0 Greenland cod because these fish were generally larger than age-1 Atlantic cod during my study.

2.2.2 Study Area

I conducted mark-recapture experiments during 2002 and 2003 in Newman Sound (48°35'N, 53°55'W; Figure 2.1), a fjord situated in Bonavista Bay on the northeast coast of Newfoundland. The fjord is 41 km long, 1.5-3.0 km wide, and divided into an inner and an outer basin. The basins are separated by a sill located approximately 7 km from the head of the fjord, rising to a depth of 18 m. Water depths reach a maximum of 55 m within the inner sound whereas outer sound depths are up to >300 m. The coastline consists of moderately exposed rocky shores interspersed with sandy coves, or pocket beaches. Nearshore substrate varies throughout the sound and ranges from mud to bedrock. Vegetation is present in the form of macroalgae (*Laminaria digitata* Lamouroux, *Agarum cribrosum* Bory, *Chondrus crispus* Stackhouse, *Fucus vesiculosus* L. and *Ascophyllum nodosum* (L.)) and eelgrass (*Zostera marina* L.), with the latter found predominantly in the subtidal region to a depth of 5-6 m, where present. Water temperatures in the study area range from 20°C in late August to -1°C in early December.

Two marking sites within the sound were used for the mark-recapture studies. I fin-clipped juvenile cod at two sites, namely Dockside (48°33.772'N, 53°57.747'W) and Buckley's Cove (48°35.406'N, 53°54.901'W); both are located in the inner sound (Figure 2.1). These sites were chosen because they were known from bi-weekly seining data to be locations of high juvenile cod abundance (Gregory et al. 1997, 2003, 2005). Both sites had eelgrass, mud-sand bottoms, and gently sloping bathymetric relief. The major difference between the two sites is that Dockside, named for its proximity to Headquarters Wharf, is a long strip of wind-exposed beach whereas Buckley's Cove is much more sheltered. An adjacent "monitoring" site was located within a few hundred metres on each side of both marking sites and used to assess short range juvenile cod movement. The monitoring sites (distance from the marking site and position in parentheses) were: Stairs Beach (248 m; 48°33.655'N, 53°57.845'W) and Whiterock (166 m; 48°33.772'N, 53°57.704'W) for Dockside, and Mistaken Cove (162 m; 48°35.347'N, 53°54.999'W) and Pipers Cove (280 m; 48°35.345'N, 53°54.692'W) for Buckley's Cove. Linear distances were converted from GPS coordinates recorded at the middle of each site. A wharf located between Dockside and Stairs Beach may act as a deterrent to juvenile cod along-shore movement. During October 2002, I fin-clipped age-0 Greenland cod at Buckley's Cove and fluorescent grit-marked age-0 Greenland cod at Dockside. Fin-clipping was used in June-July, 2003, to mark age-1 Atlantic cod at both Buckley's Cove and Dockside. Logistical difficulties prevented mark-recapture experimentation in other potential juvenile cod habitats (e.g., mud, sand) because bare substrate sites did not consistently produce adequate cod concentrations for marking

purposes.

2.2.3 Beach Seining

Beach seining (modified from Lear et al. 1980; Methven and Schneider 1998) was used to collect juvenile cod for marking. The gear used was a 25 m modified Danish beach seine with a 19 mm stretch mesh, a 24.4 m headrope, and a 26.2 m footrope. Each wing had 75 cm aluminum spreading bars that were 25 mm in diameter. The seine was deployed from a 6 m boat at a distance of 55 m from shore, and retrieved by two people standing at landmarks approximately 16 m apart on shore. The area sampled was approximately 880 m^2. Chain link on the footrope and a reduced number of floats on the headrope allowed the net to be dragged along the bottom and it sampled 2 m up into the water column. SCUBA surveillance has demonstrated that the seine effectively collects 95% of the fish present in the sample area (Gotceitas et al. 1997). During Fall 2002, all fish collected were put into fish tubs filled with seawater, identified, and separated into two groups: age-0 Greenland cod and non-age-0 Greenland cod. The two groups were kept in separate tubs until all seining was completed. Cod were identified to age class, based on age-length values given in Dalley and Anderson (1997): age-0: ≤ 100 mm standard length (SL), age-1: 100 – 200 mmSL, age-2: 200-300 mmSL, and age-3+: >300 mmSL. Fresh seawater was regularly added to the tubs to replenish dissolved oxygen. Seining continued until an acceptable number of juvenile cod ($n \approx 300$) were collected. The non-juvenile cod group was released back into the collection site after seining was completed. The procedure was repeated for age-1 Atlantic cod during Spring 2003.

2.2.4 Fin-clipping and fluorescent grit marking of age-0 Greenland cod

On October 2, 4, and 6, 2002, I fin-clipped and successfully released 331 (mean length±standard deviation; 90.7±5.8 mmSL), 197 (95.0±5.6 mmSL), and 290 (96.1±5.4 mmSL) juvenile Greenland cod, respectively, at Buckley's Cove. Each day I applied an unique partial fin-clip to collected cod. The fins used were the upper caudal lobe (Oct. 2), the first anal fin (Oct.4), and the left pelvic fin (Oct.6). Recaptured cod were not removed from the system, but instead given the fin-clip unique for that particular day. This resulted in the possibility of a single individual having as many as three fin-clips. After marking, I transferred the cod to two 70 L holding containers situated in the nearshore (depth = 1.0 m at low tide) for recovery. Each holding tank had two 10 cm x 10 cm openings covered with semi-rigid black polyethylene netting with a mesh size of 6 mm^2 to allow for water flow. Once all marking was completed, the holding containers were checked for stressed, injured, or dead cod and causalities, comprising less than 1% of cod marked, were removed. Healthy marked cod were released simultaneously at the site of capture. Two individuals marked all cod to reduce differential handling stress. Subsamples of individuals were measured to mmSL. I began monitoring for recaptures at Buckley's Cove, Mistaken Cove, and Pipers Cove on the day of the second marking event (Oct. 4). Subsequent monitoring was conducted on October 6, 8, 14, and 18. Monitoring ceased on October 18 as a result of deteriorating weather. The number of seines pulled per day for each site is tabulated in Appendix 1 (Table A1).

On October 3, 2002, I marked 286 (90.8±6.8 mmSL) age-0 Greenland cod with

fluorescent grit at Dockside. Cod were collected and transferred to a mesh-bottomed (semi-rigid polyethylene netting with 6 mm^2 mesh size) fish tub nestled into a second fish tub filled with fresh seawater. Corona magenta (pink) grit (Day GLO Colour Corp., Cleveland, OH, USA) was directed into the dermis, following the method of Phinney et al. (1967), with a commercial grit gun retrofitted with a 5 mm orifice and attached cannister for grit storage. The marking gun and the cannister were secured to an 80 ft^3 SCUBA tank with a high pressure hose. Reduction of the air pressure to 80 pounds per square inch (psi) was accomplished by a 250 psi SCUBA tank regulator. Grit application involved spraying of the cod for 2-3 seconds in the mesh-bottomed tub immediately after it was lifted out of the water a few centimetres. The gun was held roughly 40 cm above the bottom of the tub. As the cod were sprayed, the tub was gently shaken to ensure even marking on each fish. I marked cod in batches of 40-50 individuals and a subsample of each batch was examined with ultraviolet light in a dark, completely enclosed tent to determine grit retention within the dermis. Once retention was deemed satisfactory, marked cod were transferred to nearshore holding cylinders for recovery. Once all marking was completed, the holding containers were checked for moribund cod. The causalities were removed and accounted for less than 1% of the total marked. Healthy marked cod were released simultaneously. A subsample was measured to determine mmSL. Dockside, Stairs Beach, and Whiterock were monitored on October 5-6 for recaptures. Monitoring ceased on October 6 after no recaptures were collected despite a large sampling effort (10 seines/site) and the high number of marked cod originally released.

2.2.5 Acute mortality assessment

Prior to the mark-recapture experiments, I conducted an acute mortality assessment to determine whether the marking techniques contributed to mortality observed for age-0 Greenland cod. On September 18, 2002, 80 juvenile cod were collected by beach seine at Stairs Beach and divided into batches of twenty. I fin-clipped 20 cod (78.6±4.9 mmSL; range 71-87 mmSL) by removing 1/6 of the upper caudal fin lobe with dissecting scissors. Twenty cod (78.1±5.3 mmSL, 71-91 mmSL) were used as fin-clip controls. I marked 20 juveniles (79.7±5.5 mmSL, 68-89 mmSL) with grit. Twenty cod (79.2±7.7 mmSL, 60-92 mmSL) were grit mark controls. All cod were measured to the nearest mmSL. I subjected the two control groups to the same handling stress with the only difference was that no mark was administered. For example, grit mark cod were sprayed with grit for 2-3 seconds whereas grit mark control cod were sprayed with compressed air for the same time period. Each treatment batch, with its respective control batch, was placed in holding tanks situated in the nearshore. I inspected the holding containers after 8, 25, 49, and 65 hours for injured or dead cod. Mortalities were removed and measured (mmSL). I discontinued the assessment after 65 hours when no further mortalities were observed. Survivors were killed to prevent contamination of the study area with marked cod. The proportion surviving over the duration of the assessment was plotted for fin-clipped cod versus controls, grit marked cod versus controls, and fin-clipped versus grit marked. A fully factorial two-way analysis of variance (ANOVA) was performed to determine whether survival differed with treatment and time (i.e., days after treatment). A non-significant difference between treatments would

rule out differential mortality associated with the type of marks used to distinguish cod groups. The results indicated that observed mortalities were attributed to handling stress rather than the application of the mark. With slight modifications to reduce air exposure and mechanical stress, both methods were accepted for mark-recapture purposes. A long term mortality study was not conducted.

Fluorescent grit marking was abandoned as a marking technique in 2002 because of two reasons: (1) few recaptures were collected on the second sampling day despite a high number of grit-marked fish released on the first day of the study, and (2) few juvenile cod were collected for marking purposes on the second day despite an extensive sampling effort. The absence of recaptures was a cause for concern. Possible explanations could include low population numbers, high movement rates, high predation risk, and/or human error. Ogilvie (2000) evaluated predation risk of grit marked age-0 cod using tank studies. He concluded that the marking technique could increase predation rates on juvenile cod. However, it is unknown if predation rates are increased for wild cod that are not confined to small areas (i.e., aquaria) with potential predators. Small population size appeared to be the main issue because later attempts to collect fish for fin-clipping at Dockside were also unsuccessful despite a large collection effort (>10 seine hauls).

2.2.6 Fin-clipping of age-1 Atlantic cod

I fin-clipped age-1 Atlantic cod at Dockside and Buckley's Cove in June, 2003. Juvenile cod were collected by beach seine and given an unique mark specific for day and site to provide information on when and where recaptured cod were caught. Three marking

events occurred at Dockside with 272 (79.6±13.4 mmSL), 209 (84.0±11.3 mmSL), and 280 (79.0±12.6 mmSL) juveniles marked and released on June 7, 10, and 13, respectively. The lower caudal, second anal, and second dorsal fins were clipped on the respective dates. Likewise, I conducted three marking events at Buckley's Cove, with 237 (85.2±14.5 mmSL), 206 (86.9±14.4 mmSL), and 238 (91.7±11.8 mmSL) juvenile cod clipped and released on June 6, 9, and 12, respectively. The upper caudal lobe, the first anal fin, and the third dorsal fin were clipped on the respective dates. Marking details are summarized in Table 2.1. The general marking procedure for each site was similar to that used for age-0 Greenland cod in 2002. Cod were partially clipped (one-sixth of the fin) with dissecting scissors and marked individuals were transferred to nearshore holding containers for recovery. Recaptured cod were given a new mark. I conducted all the marking with one other trained person. Once all cod were marked, fatalities (<1% of cod marked) were removed prior to mass release of healthy juveniles. Monitoring for recaptures began on the second marking day and discontinued on July 17 when low capture abundances were observed. Low catches possibly resulted from juveniles migrating to deeper, cooler water after nearshore water temperatures rose to approximately 10°C. The length (mmSL) and type of fin-clip were recorded for recaptured specimens. The number of seines pulled per day for each site is tabulated in Appendix 1 (Tables A2-A3).

2.2.7 Jolly-Seber notation, formulae, and assumptions

I used the "Jolly-Seber open population" method to determine the survival of juvenile cod. Survival rates and other ecologically important parameters were calculated using the

program JOLLY (Hines 1988; Pollock et al. 1990). Jolly-Seber notation, formulae and estimation methods (Appendix 2) followed that described by Seber (1982) and reviewed by Pollock et al. (1990). The method estimates parameters for open populations whereby changes occur as a result of recruitment (births and immigration) and losses (deaths and emigration). An extension of the Petersen population estimation technique, the Jolly-Seber method involves the application of time-specific marks or tags to animals over the duration of several marking events. The procedure permits the determination of population size, survival, and influx rates; however, unbiased estimates are not achievable unless several explicit assumptions are met:

(1) Every organism in the population has the same probability of capture (i.e., equal catchability) in the *i*-th sample, regardless of whether it is marked or unmarked.

(2) Every marked organism has the same probability of surviving from the *i*-th sample to the (*i*+1)th sample.

(3) Lost or overlooked marks are negligible.

(4) Time required to sample is negligible relative to the time intervals between sampling periods.

2.2.8 Determination of survival of juvenile cod using the Jolly-Seber method

Mark-recapture data for juvenile cod at the Buckley's Cove and Dockside study areas for Fall 2002 and Spring 2003 were entered into the program JOLLY in capture-history format. This format required the capture-history of each individual to be known and entered as binary code, whereby a capture event is recorded as "1" and a non-capture recorded as "0".

Sometimes a capture event for a particular animal was recorded as a "2" meaning that the animal was collected, but not released. For example, a capture-history of 1102 indicates the animal was collected during sample times 1 and 2, not observed at 3, then caught and not released during 4. The capture-histories are used to generate the Method B tables (Leslie and Chitty 1951) in JOLLY (Appendix 3; Tables A4-A7). Data sets were analysed using the full model (A), constant removal (model B), and constant removal and survival (model D) as described in Appendix 2. Each data set provided estimates of the parameters in question (N_i, M_i, ϕ_i, B_i, and p_i); however, small sample sizes prevented good-of-fit tests to be conducted, indicating the estimates were biased. Mark-recapture results for age-0 Greenland cod at Buckley's Cove, 2002, could not provide parameter estimates with JOLLY; however, estimates could be determined for age-1 Atlantic cod at Buckley's Cove and Dockside, 2003, when the data sets were pooled. Prior to pooling the data, I performed t-tests assuming unequal variances to determine if the mean standard lengths of subsampled cod from both sites differed. Juvenile cod from the first two marking events (Days 0 and 3) were not significantly different; however, mean lengths differed for the third marking events (Day 6). To determine if size-selective sampling and mortality were possibly occurring at either site, I used the Kolmogorov-Smirnov (K-S) test for two populations to compare size class distributions of subsampled cod and cod recaptured during the next subsequent sample period. Each comparison indicated similar size-class distributions, except for cod marked at Dockside during the first marking event (Figures 2.2 and 2.3, Table 2.2). It appeared that larger cod than those subsampled were being recaptured; however, when the subsampled cod

were adjusted for daily growth [0.685mmSL day^{-1} for Atlantic cod, Newman Sound, 2002; Ings (2005)], the K-S tests indicated that the size-class distributions were not significantly different. Ings (2005) determined the growth rate by regressing the mode of daily size distributions for a pulse of newly settled age-0 cod with time; the modal lengths of 57, 66, 75, 78, 90, and 90 mmSL were observed for the Julian dates of 143, 162, 178, 179, 191, and 192, respectively. The K-S tests provided no evidence that size-selective sampling and mortality were present, hence data from the sites were pooled.

Parameter estimates from the Jolly-Seber full model (Model A) were deemed most appropriate for the pooled data according to program JOLLY. The program's goodness-of-fit tests rejected B and D as acceptable models, indicating juvenile cod do not experience constant survival or capture probability over time. Model A provided a mean survival rate estimate per day (ϕ_x) for age-1 Atlantic cod and this variable was converted to daily instantaneous total mortality (Z_i) with the equation:

$$Z_i = -\ln(\phi_x) \qquad (2.1)$$

Because the survival rate included losses attributed to death and emigration, the computed Z_i computed was positively biased. Incorporation of estimates of handling mortality and migration into Z_i reduced the bias and provided an estimate closer to the true survival. Age-1 Atlantic cod inhabiting the nearshore of Newman Sound were not recruited to the fishery, and the fishing mortality was therefore assumed to be zero; Z_i was thus equal to M_i, the daily natural mortality rate.

2.3 Results

2.3.1 Juvenile cod natural mortality hypothesis

A review of Atlantic cod natural mortality estimates in the literature indicated that early life stages, particularly eggs and larvae, have high daily mortality rates compared to juveniles and adults (Figure 2.4). For the egg stage, M ranged from 0.027-0.55 day^{-1} (Table 2.3) with a mean of 0.21 day^{-1} whereas larval mortality was only slightly lower (mean = 0.11 day^{-1}, range = 0.031-0.26 day^{-1}). Juveniles, aged 0 to 4 years old, typically experience lower mortality, with a mean of 0.029 day^{-1} (range = 0.00019-0.26 day^{-1}). Adult Atlantic cod, age 5+, have the highest survival; however, it is important to note that adult mortality was based on only five data points for which the average value was 0.00067 day^{-1} (range = 0.00041-0.0011 day^{-1}) or 0.25 $year^{-1}$. Annual M of age-5+ (exploitable) fish is commonly assumed as 0.2 $year^{-1}$.

Three life stages - eggs, larvae, adults - exhibited poor model fit to a straight line with r^2 values of 0.0055, 0.24, and 0.12, respectively (Figure 2.4). Furthermore, the egg and adult stage models were non-significant (egg: $\chi^2<0.01$, df=3, p=0.95; adult: $\chi^2=0.40$, df=3, p=0.53). The larval mortality model ($M=e^{-0.70Age\ +0.29}$) was significant ($\chi^2=4.88$, df=3, p=0.027). The juvenile stage was observed to have a significant age-dependent mortality model ($M=e^{-2.47Age\ +\ 10.39}$; $\chi^2=28.22$, df=3, $p<0.0001$; Appendix 4) with relatively high goodness-of-fit ($r^2 = 0.82$). The model residuals were normal, independent, and homogenous (Appendix 4). This model provides a mortality estimate for juvenile cod inhabiting the nearshore of Newman Sound. Using the juvenile mortality model, the predicted daily

mortality for Atlantic cod that were approximately 425 days old, if spawning was assumed to occur during April 2002, was 0.010 day^{-1}. The mortality of age-0 Greenland cod approximately 210 days old was estimated as 0.060 day^{-1}.

2.3.2 Alongshore movement of juvenile cod

Regardless of species, age, and season, juvenile cod remained near the site of release, rarely venturing further than a few hundred metres (Figure 2.5). Of 64 age-0 Greenland cod recaptured during October, 2002, 71% (n=46) were netted at the Buckley's Cove marking site with 14% (n=9) recaptured at each of the adjacent monitoring sites. Though more seines were hauled at the marking site to collect cod for fin-clipping during the first two monitoring dates, large numbers of cod were also collected at the adjacent sites. Compared to Buckley's Cove (n=807), cod abundances at Mistaken Cove and Pipers Cove were 446 and 1101, respectively, yet few recaptures were observed. No recaptures occurred at the sites in Newman Sound that were concurrently sampled on a bi-weekly basis from October 2 to November 21, 2002 (Figure 2.1), despite the collection of 1698 age-0 Greenland cod in a total of 52 seines. Similarly, age-1 Atlantic cod fin-clipped at Buckley's Cove and Dockside in June, 2003, were never recaptured beyond 280 metres from their point of initial release. The majority of cod stayed near the points of release. Of 111 total recaptures, 96% occurred at Buckley's Cove with 2% netted at each of the proximate monitoring sites. Juvenile cod at the Dockside marking site moved slightly more along shore with 2% and 4% of 82 recaptures observed at Stairs Beach and Whiterock respectively. Sampling effort differed among the sampling sites, but more cod were collected at the marking sites than the

adjacent sites in 2003 than in 2002. When the data were not standardized for sampling effort, the abundances of cod collected at Buckley's Cove, Mistaken Cove, and Pipers Cove, were 697, 384, and 390, respectively; cod abundances for Dockside, Stairs Beach, and Whiterock were 690, 238, and 270, respectively. Standardization of the data, through the inclusion of only cod netted in the first collection seine, provided a similar picture of juvenile cod movement patterns. Of 43 total recaptures collected in the first seine, 98% occurred at Buckley's Cove with 2% and 0% at Mistaken Cove and Pipers Cove respectively. Similarly, 78% of 23 first seine recaptures were taken at Dockside while only 9% and 13% were taken at Stairs Beach and Whiterock respectively.

Dispersal to adjacent sites would be expected to increase with time, but this did not occur (Figure 2.5). Age-0 Greenland cod recaptures were consistently highest at the marking site over the 17 days (Oct. 2-18) of the Fall 2002 study. The mark-recapture studies conducted at Buckley's Cove and Dockside in Spring 2003 were twice as long in duration with 41 (June 6-July 17) and 40 days (June 7-July 17) respectively; yet the capture frequencies remained high at the marking sites. It would be expected that the likelihood of collecting a fin-clipped cod outside the release sites during bi-weekly seining would increase as time progressed; however, no marked cod were recaptured outside of the marking locations despite extensive sampling.

2.3.3 Acute mortality assessment of juvenile cod marking techniques

The acute mortality assessment determined that the fin-clips and grit marks administered to the juvenile cod were not the major cause of death. After assuming normal distribution, a test of survival against treatment (fin-clipped cod, fin-clipped control cod) time

(i.e., days after treatment), and the interaction between the two indicated that survival was not significant different between the treatments over the duration of the assessment (Figure 2.6; treatment term χ^2=1.71, p=0.191, df=1). Though overall percent survival differed by nearly 25%, a similar test showed that the difference between the grit-marked cod group and grit-marked control cod group was also non-significant (treatment term χ^2=2.39, p=0.122, df=1). Furthermore, the survivorship of the fin-clipped cod did not differ significantly from the grit-marked cod survivorship (treatment term χ^2=0.91, p=0.341, df=1). Non-significance of the interaction terms indicated that changes in survival over time was also similar between the treatment groups (fin-clipped cod vs fin-clipped control cod: χ^2=0.16, p=0.685, df=1; grit-marked cod vs grit-marked control cod: χ^2=2.92, p=0.087, df=1; fin-clipped cod vs grit-marked control cod: χ^2=0.090, p=0.770, df=1). No mortalities were observed for most treatments (fin-clipped, fin-clip control, and grit-marked) after 49 hours. Cod appeared to be in good condition when the study ceased after 65 hours. Although survival amongst the treatments was not significantly different, overall mortality was high (~50%), possibly resulting from handling and containment stress. Like survivorship, the differences in mean length of fin-clipped cod (two-tailed t-test assuming unequal variances; t=-0.278, df=38, p=0.782) and grit-marked cod (t=0.213, df=36, p=0.832) with respect to their controls were non-significant. Mean standard lengths of the treatment fish were also similar (t=-0.681, df=36, p=0.500).

Mortality was significantly higher for small cod than relatively larger cod in the acute mortality experiment (Figure 2.6). The K-S test provided strong evidence (D=0.453,

$p<0.001$) against the null hypothesis of similar length distributions of the cohorts. During the assessment, the largest number of mortalities was observed for cod grouped in the 75-79 mmSL size class (n = 17). For next size class (80-84 mmSL), the number of mortalities are noticeably lower (n = 7). The highest number of survivors (n = 13) belonged to the 80-84 mmSL size class, followed by cod belonging to the 75-79 mmSL (n = 11) and 85-90 mmSL group intervals (n=11). Differential mortality was determined to be negatively affecting juvenile cod less than 80 mmSL because the probability of surviving was higher for cod ≥80 mmSL. For example, 79% of the observed mortalities (n = 39) were <80 mmSL while 66% of the surviving cod (n = 41) were ≥80 mmSL. Differential mortality may be an issue for field experimentation because roughly 40% of the juvenile cod I marked were smaller than 80 mmSL. During the assessment, the possible factors contributing to mortality include collection, handling, and containment stress; however, the precise cause was unknown.

2.3.4 Jolly-Seber parameter estimates

Data collected for juvenile Greenland cod and Atlantic cod were insufficient for analysis with the program JOLLY. When the recaptures were entered separately for Buckley's Cove Fall 2002, Buckley's Cove Spring 2003, and Dockside Spring 2003, JOLLY output parameters indicated that goodness-of-fit tests could not be determined for Models A, B, and D (Table 2.4). Failure to determine an appropriate test for juvenile cod was probably due to the small sample sizes at each site. Although not possible for age-0 Greenland cod at Buckley's Cove in Fall 2002, pooling the recapture data for age-1 Atlantic cod at Buckley's Cove and Dockside in Spring 2003 provided a sample size large enough for JOLLY analysis.

The goodness-of-fit test rejected Models B and D as appropriate estimators of juvenile cod survival because of significantly large chi-square values (Model B: χ^2=6.81, df=2, p=0.033; Model D: χ^2=22.18, df=4, p<0.001). Furthermore, both B and D, the simpler models, were rejected when compared to Model A, the full model (B vs. A: χ^2=4.74, df=1, p=0.029; D vs. A: χ^2=20.12, df=3, p<0.001). I therefore used estimates and confidence limits from Model A (χ^2=2.07, df=1, p=0.150) to describe the population ecology of juvenile Atlantic cod. Rejection of models B and D indicate that survival and probability of capture varies with time for age-1 Atlantic cod in nearshore habitats of Newman Sound. Parameter estimates for Model A, with standard errors and confidence intervals, are provided in Table 2.5.

Mean daily apparent survival for age-1 Atlantic cod was estimated as 0.91±0.055 day^{-1} with 95% confidence intervals of 0.80-1.0 day^{-1}. The estimate is equivalent to an M of 0.095 day^{-1} (95% confidence limit = 0.018-0.22 day^{-1}), nearly an order of magnitude higher than the expected mortality rate of 0.010 day^{-1}. Apparent mortality overestimates true mortality because the survival value includes both migration and handling mortality. Percent migration for the pooled data in Spring 2003 was estimated as 5% and the estimate was used to adjust the mortality rate from the Jolly-Seber method. The acute mortality assessment showed that cod <80 mmSL had a higher mortality rate compared to cod ≥80mmSL. Approximately 60% of the cod marked and released in Spring 2003 were 80 mmSL or longer. In total, 49% of the 80 cod used in the assessment died. If cod >80 mmSL are excluded from the analysis, the percent mortality after approximately three days increases to 69%. However, if cod <80 mmSL are excluded, the percent mortality decreases to 23%. Because marked cod

were generally longer than 80 mmSL during the field study, the apparent M was adjusted using the lowest percent acute mortality estimate. Exclusion of migration and handling mortality estimates lowers the mortality rate to 0.068 day^{-1} with 95% confidence limits of 0.013-0.16 day^{-1}. The observed M is equivalent to approximately 660 juvenile cod surviving out of 1000 after a period of one week. The expected mortality value of 0.010 day^{-1} (i.e., approximately 940 surviving after one week) does not fall within the confidence limits of the observed value, indicating the estimates are significantly higher than the predicted based on age.

2.3.5 Validation of Jolly-Seber assumptions

Statistical validation of equal probability of catch (Assumption #1) was not possible because of small sample size even when data were pooled. Biological intuition was used to justify the equal catchability assumption. Juvenile cod were observed to be limited to short migrations of a few hundred metres and remained near a given study site. Therefore, it is unlikely that marked cod permanently left the study area, a phenomenon that would reduce catchability. Certain sampling gears can cause marked individuals to have trap-friendly or trap-shy responses that increase or decrease respectively the probability of recapture. Beach seining is an active sampling gear that offers no reward with capture. Furthermore, some cod were recaptured multiple times, suggesting that gear avoidance was minimal. One problem with beach seining is that the entire site cannot be sampled effectively because submerged obstructions and(or) the layout of the shoreline may prevent successful net retrieval. Furthermore, cod may inhabit waters beyond the sampling range of a hand-pulled seine.

Depths of 5-10 m are typically inhabited by age-0 cod in summer and fall (Cote et al. 2001) and by age-1 cod during spring (personal observation), presumably to minimize distributional overlap with older, larger conspecifics patrolling deeper waters (Linehan et al. 2001). In addition, eelgrass beds in Newman Sound typically extend to depths of 6-7 m. The deepest site I monitored had a maximum depth of 5 m at the farthest extent of the seine, therefore some areas where juvenile cod and eelgrass may be distributed were not effectively sampled. Implementation of other sampling gears can determine whether some cod are inaccessible to the seining gear; however, beach seining was the only sampling gear used. Cod were not observed to leave the study sites; however, variability in catches from seine to seine (Figure 2.8) suggests that cod move around within the site from gear inaccessible areas to accessible areas. There was neither statistical nor biological evidence for unequal catchability.

Differential mortality among marked juvenile cod (Assumption #2) appeared to be negligible. Table 2.6 shows that 14 fin-clip combinations were used during Spring 2003. The assumption of survival homogeneity requires that all marked cod released, regardless of number of clips present per individual, must have the same probability of mortality. Some fin-clips, particularly the single caudal marks, were recaptured more frequently than other combinations because a higher abundance of caudal clipped individuals were released and present in the wild for a longer time period. To determine if certain fin-clip combinations had a higher probability of recapture, the recapture percentage for each respective combination (i.e., number of single caudal clips recaptured at time i/number of single caudal clipped cod present in the wild at time i-1) was calculated for each sampling period. Because

some fin-clip combinations were in the wild for a longer time period, the mean fin-clip percentage was determined and compared to assess whether differential mortality was present (Figure 2.9). Overall, mean fin-clip combination percent recapture ranged from 0% to 4%. Two fin-clip combinations (lower caudal-second anal-second dorsal and first anal-third dorsal) were not recaptured; however, very few cod possessed these marks (3 and 4, respectively), suggesting that extremely low abundance, not mark-related mortality, affected the probability of being re-encountered. Furthermore, it could be assumed that multiple marked cod would have a lower survival compared to cod with single marks; however, multiple marked cod [n = 18, mean length ± standard deviation = 92.6 ± 9.3 mmSL, range = 79 - 112 mmSL] had mean recapture percentages similar to single marked cod [n = 174, mean length = 92.6 ± 11.6 mmSL, range = 56 - 115 mmSL] during this study. These observations suggest that differential fin-clip mortality did not occur, which is surprising because the acute mortality assessment indicated that handling mortality may be high in the field. However, increased experience with the marking technique over time may have decreased handling stress, allowing multiple marked cod to survive despite repeated recapture. The mortality estimates determined for the marked population can also be extended to the whole population because marked cod were observed to have survival rates equivalent to unmarked cod (Figure 2.5).

Estimation bias attributed to lost or overlooked marks (Assumption #3) was judged to be negligible. No evidence of fin regeneration was apparent for cod during the acute mortality assessment, nor for recaptured cod that were in the wild for several weeks. All

juvenile cod were examined for fin-clips by experienced field staff and no identifications were conducted by others (e.g., commercial and recreational fishermen). One problem with the marking method is that naturally occurring injuries sustained from predation encounters may obscure clipped fins. This could result in misidentification - mistaking a natural injury for a fin-clip - or the overlooking of clips because an injured fin may have been initially marked. One component of the sampling protocol was to note any marks that were questionable; however, such marks comprised less than 1% of all cod examined.

During my study, the time required to sample was negligible relative to the time between sampling periods (Assumption #4). Figure 2.10 shows the trend of total catch and recapture percentage with time for standardized and unstandardized collection data. Despite differing sampling intensities that produced variable cod abundances, percent recapture remained fairly constant over the duration of the studies. Trends of increases in recaptures with time were observed at Buckley's Cove in 2002 and 2003, largely because percent recapture was highest on the last days of sampling despite a decline in total cod caught (5 and 6, respectively). Overall, the trends suggest that marked cod randomly dispersed within the unmarked population and that the time required for seining (i.e., several hours) was negligible compared to the time between collection periods (i.e., several days).

2.4 Discussion

Juvenile cod in nearshore Newman Sound experience a natural mortality rate of $M=0.068\ day^{-1}$ in areas with eelgrass habitat. It is unknown if this value is high relative to other habitats because logistical difficulties prevented survival rate determination in other

potential juvenile cod habitats. Bare substrate (e.g., sand, mud) sites did not consistently produce adequate cod concentrations for mark-recapture purposes. Juvenile cod rarely frequent such habitats; however, when present, they are usually in high abundance because of aggregatory behaviour (Laurel et al. 2004). Cod residency is probably of short duration and the probability of recapture would be extremely low, thereby making marking impractical. Consistently low abundances in bare substrate sites may indicate that predation risk greatly outweighs foraging efficiency and that mortality is high relative to eelgrass (Gorman 2004). Other habitats, such as macroalgae and cobble, were located in areas of high wind and wave exposure and could not be sampled by beach seining. Studies have been not conducted to estimate the natural mortality of young cod in these habitats; however, tethering studies suggest cobble and bedrock habitats may be very risky for juvenile cod compared to eelgrass habitat (Gregory et al. in prep.).

The natural mortality rate of juvenile cod in coastal Newman Sound was higher than estimates reported for cod of similar ages in other regions. Ottera et al. (1999b) reported mortalities of 0.0043-0.0071 day^{-1} for juvenile cod tagged and released in the Øygarden archipelago of western Norway. However, the cod released by these authors were larger (length range=25-40 cm) than those fin-clipped in Newman Sound and therefore would be expected to have a higher survival rate. Age-1 Georges Bank cod also exhibit lower mortality rates (0.025 to 0.038 day^{-1}; Serchuk et al. 1994); however, a direct comparison between the estimates is not feasible because specific lengths were not reported in that study.

Despite adjustments for dispersal and handling mortality, the observed mortality rate was significantly higher than expected for juvenile cod. Jolly-Seber parameter estimates can be biased if model assumptions are false. Heterogeneity of capture probability is typical of natural populations (Caughley 1977; Carothers 1979). The equal catchability assumption can be violated if marked individuals have a lower capture probability than the unmarked population (Pollock et al. 1990). A low average capture probability will cause the marked population size to be underestimated and the survival estimate will be negatively biased (Pollock et al. 1990). Statistical tests could not refute the possibilty of unequal catchability of juvenile cod because data were insufficient. However, unequal catchability may have occurred if the efficiency of the sampling method to recapture marked cod depended on body size, a factor that requires testing for the type of beach seine used during my study. Furthermore, assuming emigration to be permanent may bias mortality rates because animals may simply be moving in and out of the study area while avoiding the sampling gear (Pollock et al. 1990). Temporary emigration can invalidate the unequal catchability assumption and cause mortality rates to be overestimated. In my study, the mortality rate observed for age-1 Atlantic cod was calculated using the minimal value for movement rates (i.e., 5%). If movement rates were higher than the minimal value, then the mortality rate would be lower than the 0.068 day^{-1} observed for age-1 Atlantic cod. For example, doubling the movement rate to 10% slightly reduces the mortality value to 0.064 day^{-1} while increasing movement to 50% greatly reduces mortality to 0.026 day^{-1}. Several authors have concluded that mean survival estimates are robust to capture heterogeneity because biases are negligible (Cormack

1972; Carothers 1973, 1979; Nichols and Pollock 1983); however, the precision of the estimates may be negatively biased (Carothers 1973; Pollock et al. 1990). Even if the variance of juvenile cod survival was underestimated, the precision should still be reliable given that the original estimate was reasonably precise. However, caution is warranted; high precision does not guarantee accurate estimates whereas low precision typically signifies that estimates are impractical (Koper and Brooks 1998).

Heterogeneous survival probabilities of marked animals will positively bias mortality estimates if marking or handling reduces survival (Pollock et al. 1990). Juvenile cod were collected with a seine net, manually handled by field personnel, and marked with fin-clips. Each component of the marking procedure can induce stress that may result in short-term or long-term mortality (Ricker 1949). Collection procedures typically subject fish to abrasive contact with the net, with the sides and(or) bottoms of holding containers, with other fish and invertebrate species, and with inadvertently entrained objects, such as woody debris (Matthews et al. 1997). Resultant effects may include mechanical damage, physiological stress, and scale loss (Matthews et al. 1997). Though fin-clipping is commonly used, there is considerable debate whether it increases mortality (Ricker 1949; Churchill 1963; Brynildson and Brynildson 1967; Coble 1971; Nicola and Cordone 1973; Mears and Hatch 1976; Haines and Modde 1996; Pratt and Fox 2002). Possible detrimental fin-clipping effects include increased predation risk, diminished competitive ability, increased susceptibility to environmental changes, increased vulnerability to pathological invasion, and altered physiological processes and(or) behaviour (Coble 1967). Studies have reported that

fin-clipping does not elevate predation risk for a variety of juvenile fish species (walleye *Stizostedion vitreum,* Churchill 1963; yellow perch *Perca flavescens,* Coble 1967; Colorado squawfish *Ptychocheilus lucius,* Haines and Modde 1996; Alantic cod, Ogilvie 2000). Furthermore, several authors have reported that fin-clipping has little effect on growth (Churchill 1963; Coble 1971; rainbow trout *Salmo gairdneri,* Nicola and Cordone 1973; muskellunge *Esox masquinongy,* McNeil and Crossman 1979; rainbow trout Gjerde and Refstie 1988; walleye, Pratt and Fox 2002), providing indirect evidence that foraging capability was not diminished. Similar recapture proportions of various fin-clip combinations suggested that heterogeneity in survival probabilities of marked individuals was absent from my study.

Further research is required to determine the mortality associated with chronic handling stress for juvenile cod. Short-term handling and containment prior to release increased the observed mortality of juvenile cod in this study; however, survival estimates were adjusted to account for the effects of such stress. Like movement, the minimal value (23%) for handling mortality was used to adjust the observed mortality rate. This value may potentially be higher because prolonged mortality directly or indirectly attributed to handling and containment stress, which was not tested, may be occurring for field released fish. For example, fish may exhibit abnormal behaviour following release after a stressful event (Mesa and Schreck 1989), which may increase susceptibility to predation, reduce feeding efficiency, and decrease resistance to disease. For instance, once released, tagged cod may swim rapidly away from the point of disturbance, irrespective of the suitability of habitat types. This high

activity may increase encounter rates with nearby predators. If it was assumed that stress-related chronic mortality was equal to stress-induced acute mortality during my study, then the actual mortality rate would be reduced to 0.047 day^{-1}. The uncertainty in estimates of delayed stress-related mortality may be a major factor contributing to the high observed mortality rates for age-1 Atlantic cod in nearshore Newman Sound.

Tag loss or misidentification causes survival estimates to be underestimated, reducing accuracy (Arnason and Mills 1981; Pollock 1981; Nichols and Hines 1993). If tags are shed or overlooked, the marked population is reduced in size and apparent loss exceeds true loss. Pollock (1981) observed that tag loss decreases precision of estimates even when the rate of loss is known and parameters are adjusted. However, tag loss and tag misidentification were negligible during my study and did not affect the survival estimate.

The natural mortality rate of juvenile cod in nearshore Newfoundland may be largely attributed to predation. In Newman Sound, tethering studies have indicated that the major predators of juvenile cod include older, larger conspecifics (Atlantic and Greenland cod), sculpins, and white hake (Linehan et al. 2001; Laurel et al. 2003). Other potential predators that are present, though in low abundance, are sea raven (*Hemitripterus americanus*; Tupper and Boutilier 1995) and thorny skate (*Raja radiata*; Palsson 1994). Intercohort cannibalism may be an important predation component, with cod as young as age-1 that are capable of consuming smaller conspecifics (Linehan et al. 2001; Laurel et al. 2003). Gape size generally determines the maximum ingestable prey size and several studies have shown that successful predators typically are twice the length of their prey (Miller et al. 1988; Bogstad et al. 1994;

Salvanes 1995; Blom and Folkvord 1998; Linehan et al. 2001). Predatory loss may not be limited to piscivorous fishes because mammalian predators, specifically harbour seals (*Phoca vitulina*) and sea otters (*Lutra lutra*), are also present. Seals in other regions consume Atlantic cod juveniles that are less than 40 cm in length (Hammill and Stenson, 2000). The impact of seal predation on the Newman Sound cod population is unknown, but is likely low because few seals frequent the sound (personal observation). Otters foraging in coastal regions of Terra Nova National Park have been observed to consume age-1 juvenile cod (mean length = 17 cm; H. Stewart, Memorial University, Department of Biology, personal communication). The inner basin of Newman Sound is a migratory bird sanctuary that supports populations of avian piscivores, including gulls, terns, mergansers, cormorants, loons, eagles, and ospreys (Linehan et al. 2001). Like seals, no studies have been conducted to determine avian predation on juvenile cod in Newman Sound. Bird predation may be significant as shown by Norwegian cod enhancement studies that routinely include searching seabird nesting areas for expelled tags. In Masfjorden, a 26 km^2 fjord, cormorants (*Phalacrocorax carbo*) and shags (*P. aristotelis*) have been recognized as important predators (Ottera et al. 1999a) and were estimated to consume 20 t of cod - primarily juveniles - over a six-month duration (Arnold Haland in Ottera et al. 1999a).

Aside from predation and cannibalism, starvation may contribute to the high mortality of Newman Sound juvenile cod. Death resulting from starvation occurs frequently in the wild (Holdway and Beamish 1984); however, this loss goes largely unnoticed (Dutil and Lambert 2000). Starvation mortality may be attributed to predation when increased

vulnerability to predation risk arises from the diminished swimming capacity of weakened fish (Dutil and Lambert 2000). Furthermore, starved fish are likely to be slow-growing and increased susceptibility to predation may be associated with poor condition when greater behavioural risks are taken to procure food items (Sogard 1997). Small juvenile cod may be more sensitive to starvation because they may lack the energetic reserves required to maintain necessary activity during prolonged periods of restricted food availability. However, it is unknown what effect that starvation may have on the Newman Sound juvenile cod population because little work has been conducted concerning food availability.

Juvenile cod exhibited short range migrations in shallow, nearshore habitats in Newman Sound, rarely venturing farther than a few hundred metres during spring and autumn. There was no evidence for extensive migration as age 0-1 cod remain localized within sheltered coves which had substrates of low bathymetric relief and structurally complex habitat (e.g., cobble, kelp, and(or) eelgrass). Juvenile cod may undertake long range "offshore" migrations into deeper waters; however, such movements are unknown because offshore sites were not sampled. Short range movements have been documented for juvenile cod in coastal areas of Newman Sound (Gotceitas et al. 1996; Gregory et al. 1997), Trinity Bay (Grant and Brown 1998), Nova Scotia (Tupper and Boutilier 1995), and the Northeast Atlantic (Hjort 1914; Svasand and Kristiansen 1990; Pihl and Ulmestrand 1993; Smedstad et al. 1994; Skreslet et al. 1999). Conversely, high rates of nearshore movement of age-0 cod in Newman Sound have been reported for areas characterised by non-convoluted shoreline and contiguous bands of structural habitat (Laurel et al. 2004) in a high density year. Low site fidelity was

attributed to density-dependent aggregatory behaviour (i.e., schooling or shoaling) when juvenile cod were forced to frequent low quality habitats after high quality habitats became saturated (Laurel et al. 2004). Density-dependent aggregatory behaviour also suggests that the availability of habitat is not limiting during years of low abundance and juvenile cod are not pressured to frequent areas of high predation risk. Juvenile cod abundances in Newman Sound were lower in 2002 (Gregory et al. 2003) and in 2003 (Gregory et al. 2005) than in previous years, which may explain why movement rates were low during the current investigation. Furthermore, movement rates may vary with season and age. Laurel et al. (2004) marked age-0 cod in late summer (August-September) whereas age-1 Atlantic cod were marked in early summer (June-July) during my study. The juveniles of several species (Greenland cod, Atlantic cod, white hake) concurrently recruit to coastal habitats of Newman Sound over a relatively short period of time in late summer (Gregory et al. 1997; personal observation). Meanwhile, age-1 Atlantic cod, presumed to overwinter in the sound, may only compete with Greenland cod for habitat during spring. Large-scale seasonal migrations are probably not undertaken by juvenile cod younger than two years old. Winter migrations by age 2-3 year Atlantic cod to deeper waters beyond inner Newman Sound does occur (Cote et al. 2004).

Juvenile cod remain localized in nearshore Newman Sound possibly because the availability of structurally complex habitats, such as eelgrass and kelp, provide predator refuges and high food densities. Several laboratory (Gotceitas and Brown 1993; Gotceitas et al. 1995; Fraser et al. 1996; Lindholm et al. 1999) and field studies (Keats et al. 1987;

Gotceitas et al. 1997; Grant and Brown 1998; Linehan et al. 2001; Laurel et al. 2003 a,b; Laurel et al. 2004) have shown that juveniles frequent eelgrass habitat to reduce predation risk. Vertical structure, such as eelgrass blades, increases survival by providing protective cover for juvenile fish from visual predators (Orth et al. 1984; Werner and Gilliam 1984), such as older conspecifics, sculpin *Myoxocephalus* spp., and white hake (Bogstad et al. 1994; Linehan et al. 2001; Laurel et al. 2003 a,b). Additionally, food densities, in particular pelagic and epiphytic zooplankton, are higher in eelgrass than in bare substrate (e.g., mud, sand) habitats (M. Renkawitz 2005, Memorial University, M.Sc. thesis, in prep.). Consequently, the abundance of piscivorous fishes is also commonly highest in vegetated areas (Linehan et al. 2001), a situation that forces younger, smaller fish to adapt strategies to optimize foraging efficiency while at risk from mortality (Werner and Gilliam 1984; Lima and Dill 1989). Some individuals may forage by adopting an activity reduction strategy that optimizes movement and subsequently the possibility of attracting nearby patrolling predators (Lima and Dill, 1989). Other juvenile cod may embrace more active foraging methods by forming aggregations (Grant and Brown 1998; Laurel et al. 2004). Utilization of different foraging tactics by members of the same cohort may explain conflicting reports on juvenile cod movement.

The declining abundance of juvenile cod over time may result from a distributional shift from shallow habitats to deeper waters. After spring, the catch-per-unit effort of age-1 Atlantic cod had diminished by July 17 (Day 40-41) at both marking sites. The apparent out-migration may have been temperature-dependent because surface waters warmed to 9-10°C,

the upper limit of the species' preferred temperature range (Scott and Scott 1988). A similar occurrence was observed for age-0 Greenland cod in the fall. Presumably this "offbeach migration" is to avoid the potential exposure to ice crystals in freezing water in autumn; such exposure is known to be fatal (Goddard et al. 1992; Goddard and Fletcher 1994). In Buckley's Cove, the majority of older juvenile Atlantic cod (age 2-3) begin an out-migration from the inner sound after water temperatures become isothermal in early November (Cote et al. 2004). Smaller juveniles may simply move to deeper waters (Methven and Bajdik 1994) because predator density, and hence risk, is reduced. Age-0 cod probably overwinter within the sound because they possess the physiological ability to withstand colder temperatures relative to older conspecifics (Kao and Fletcher 1988; Goddard et al. 1992). Grant and Brown (1998) speculate that juvenile cod remain localized in nearshore Trinity Bay during their first winter.

In summary, juvenile cod experience a high mortality rate ($M = 0.068\ day^{-1}$) relative to predictions based on age and life history stage. High mortality associated with eelgrass may suggest that juvenile cod abundance is low in other habitats (e.g., mud, sand) because the risk of mortality is even greater, though other factors, such as food abundance and abiotic conditions, may also play significant roles. The natural mortality of juvenile cod may be largely attributed to predation, including cannibalism; however the high mortality rate may also be attributed to uncertainties in onshore-offshore movements and(or) chronic handling stress. Mark-recapture experimentation indicate that movement rates are low for juvenile Atlantic and Greenland cod in eelgrass habitat during years of low cod abundance. The

movement rates of cod aged 0-1 years are likely dependent on population dynamics because site fidelity has also been observed to be low when cod densities are high (Laurel et al. 2004). Low movement rates within eelgrass suggest that conservation of such nursery habitat is extremely important for juvenile cod when population sizes are small.

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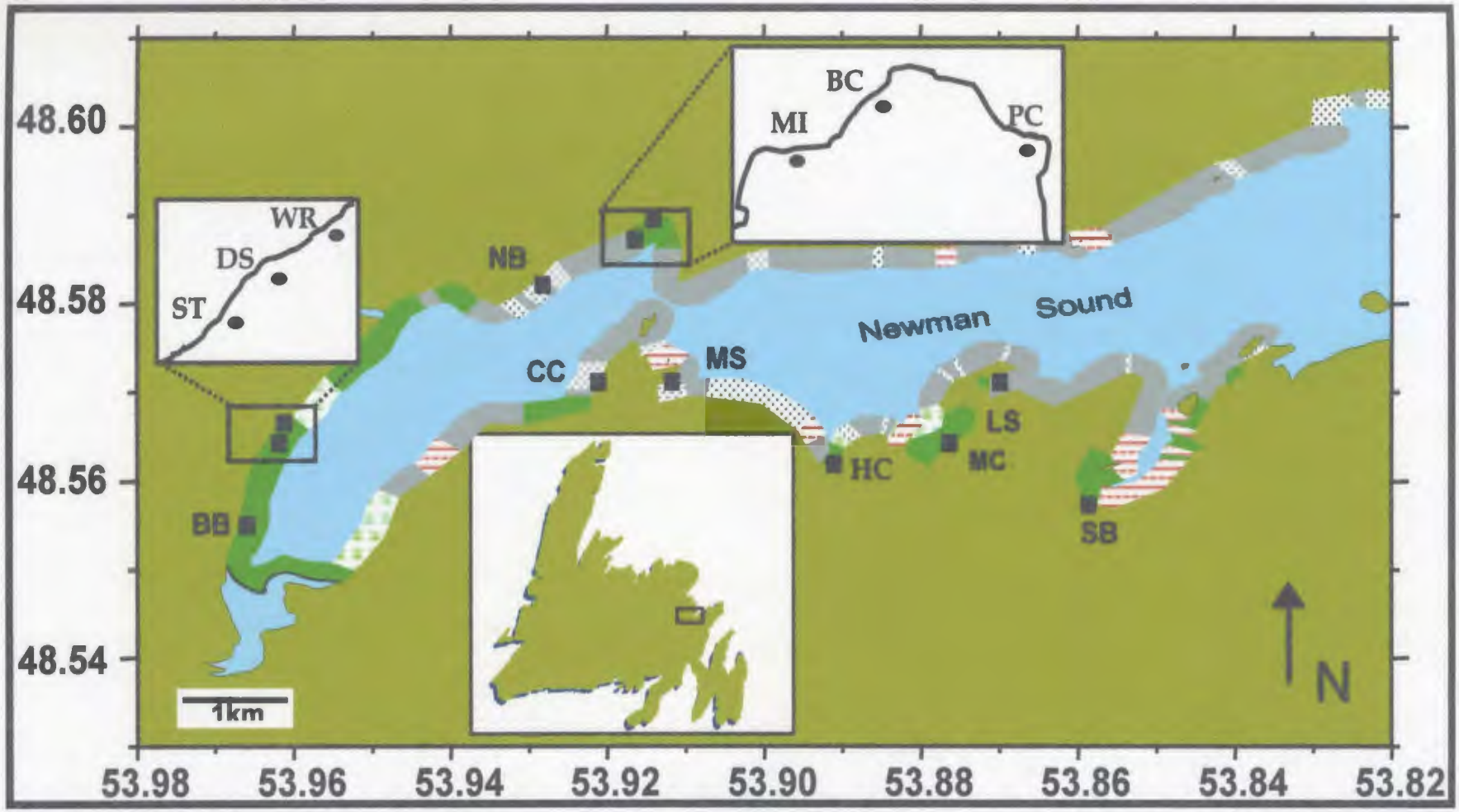

Figure 2.1: Map of the study area, Newman Sound, Bonavista Bay, Newfoundland. The two marking areas - Dockside (DS) and Buckley's Cove (BC) - are enlarged with the marking and adjacent monitoring sites depicted as circles. Also featured are 13 bi-weekly seining sites, represented as squares. Nine bi-weekly sites [Big Brook (BB), DS, Whiterock (WR), Bermuda Beach (BE), Mistaken Cove (MI), BC, Hefferns Cove (HC), Minchins Cove (MC), and South Broad Cove (SB)] have eelgrass habitat, shown with light green colouration, while the remaining four [Cannings Cove (CC), Newbridge Cove (NB), Mount Stamford (MS), and Little South Broad Cove (LS)] have no appreciable eelgrass.

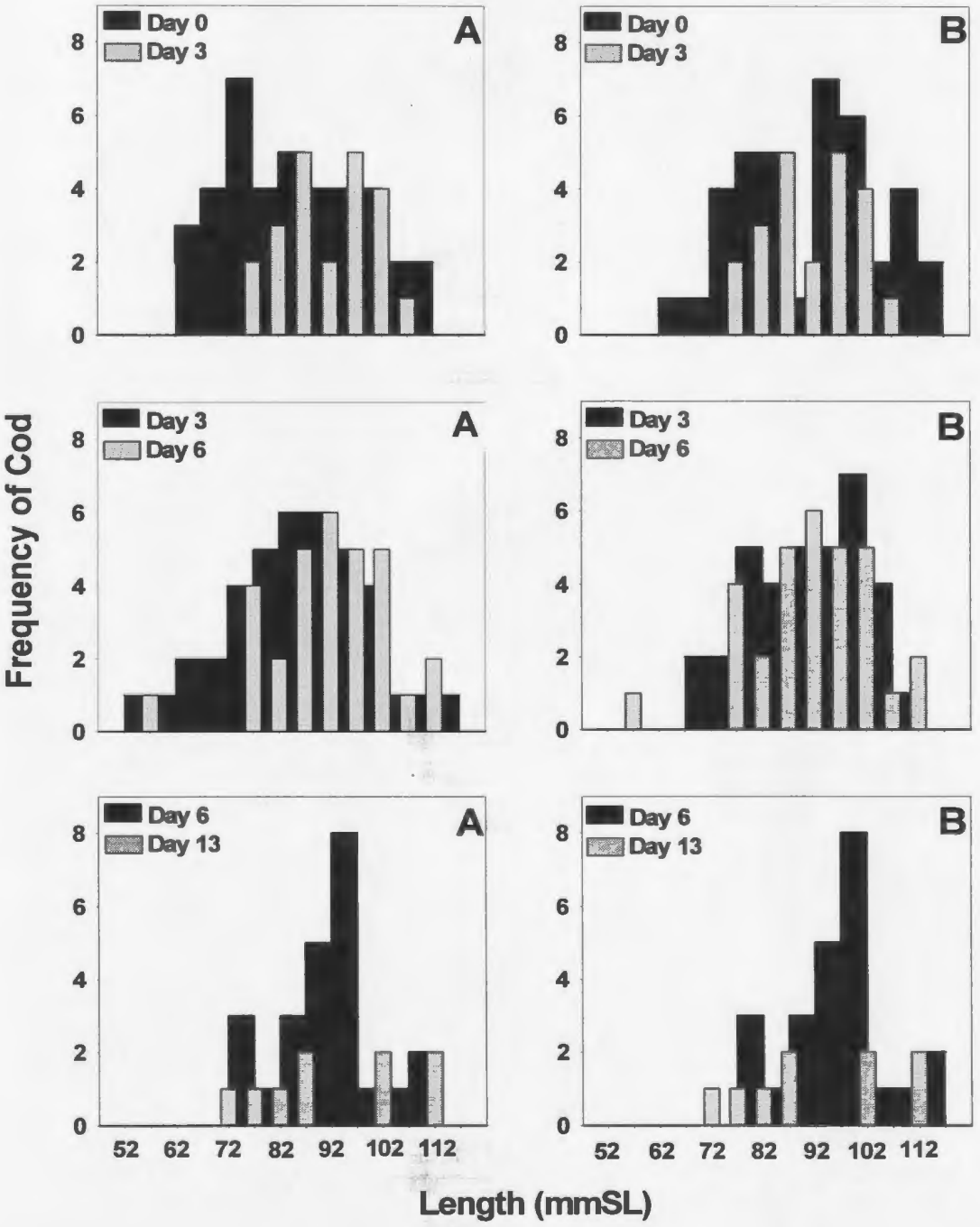

Figure 2.2: A comparison of length-frequency distributions of subsampled cod (black bars) and cod recaptured during the subsequent sampling period (grey bars) at Buckley's Cove during Spring 2003. Distributions in graph **A** are original lengths whereas graph **B** depicts the lengths of subsampled cod after adjustment for daily growth.

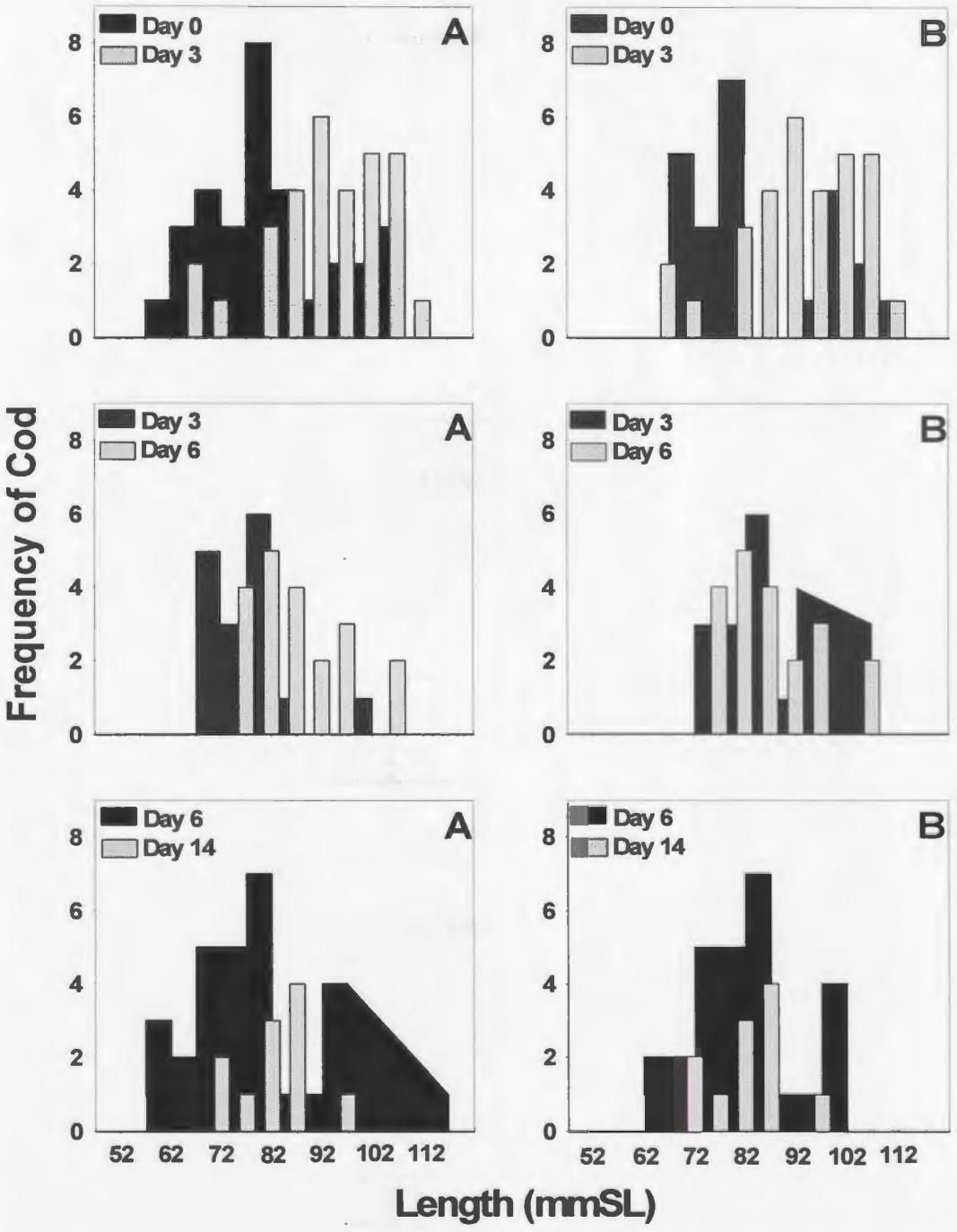

Figure 2.3: A comparison of length-frequency distributions of subsampled cod (black bars) and cod recaptured during the subsequent sampling period (grey bars) at Dockside during Spring 2003. Distributions in graph A are original lengths, and lengths of subsampled cod were adjusted for daily growth in graph B.

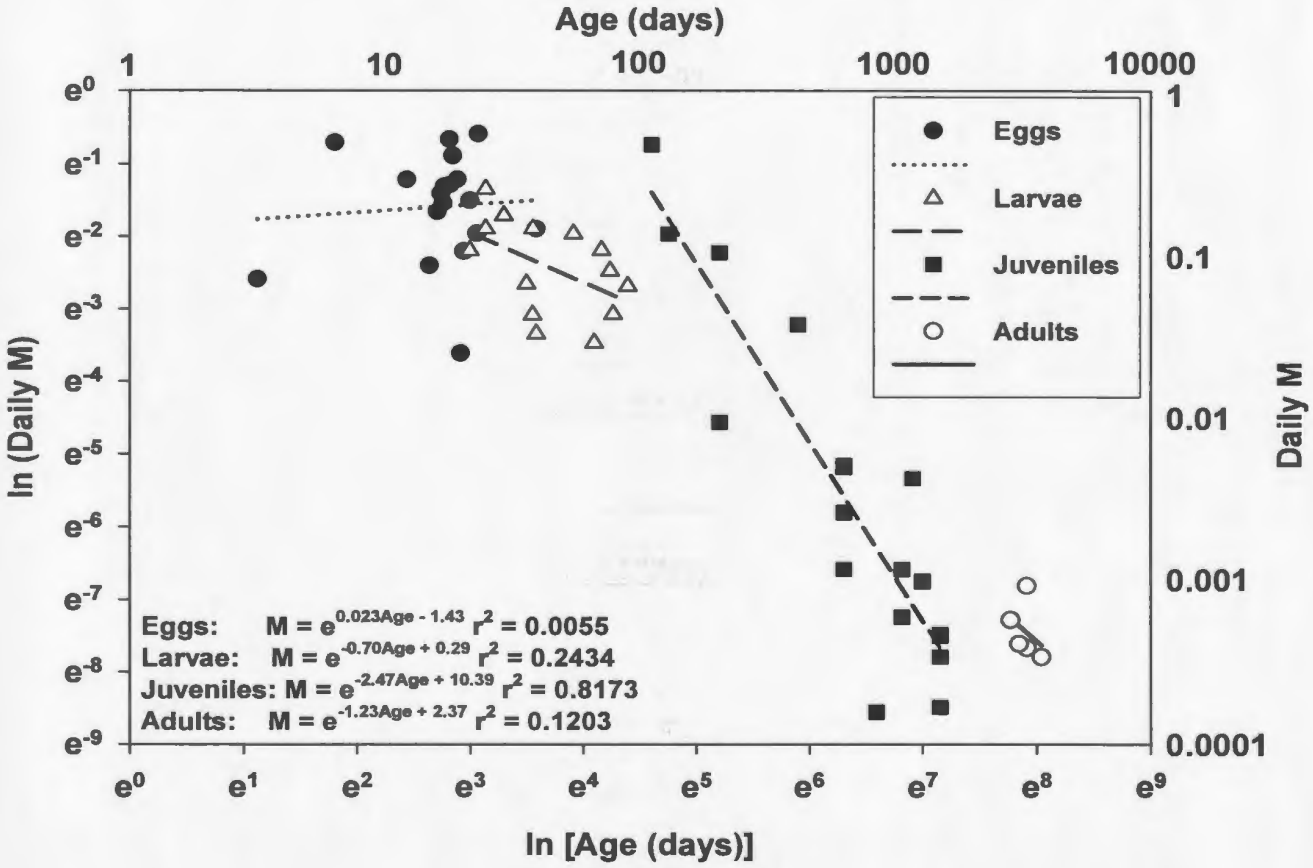

Figure 2.4: The daily instantaneous natural mortality rates (M) of the life history stages of Atlantic cod (*Gadus morhua*). The data was broken into four groups (eggs, larvae, juveniles age 0-4, adults age 5+) because a regression of all data combined revealed a non-linear relationship on a log-log scale. Goodness-of-fit to a power law was poor for all stages, except juveniles.

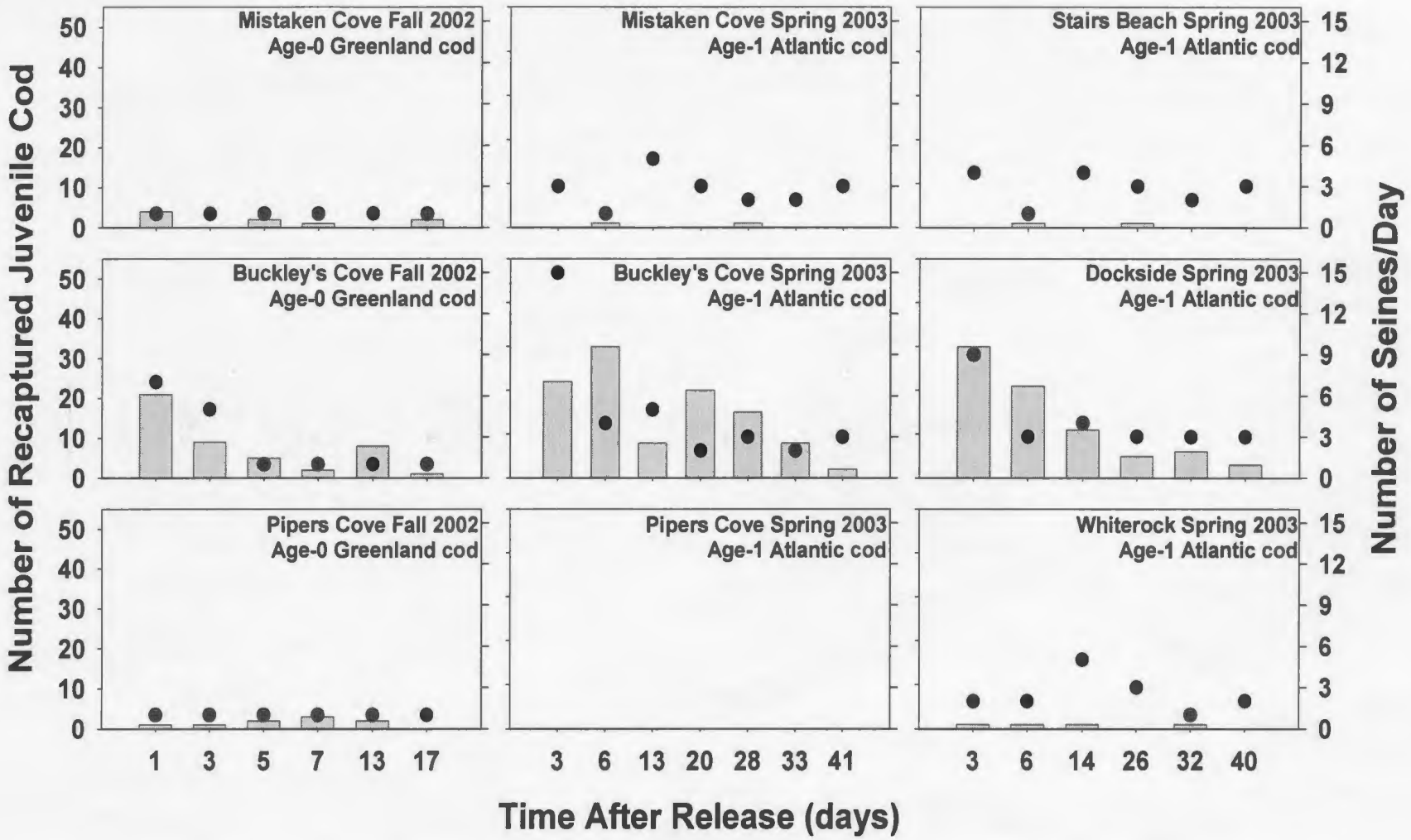

Figure 2.5: Alongshore movement of juvenile cod appears limited with the majority of fin-clipped cod recaptured (grey bars) at the site of release (middle graphs). Few recaptures were collected at adjacent monitoring sites (top and bottom graphs). Sampling intensity, expressed as the number of seines per sampling day (solid black diamonds), varied over the duration of the study. Age-0 Greenland cod were marked and released in Fall 2002 whereas marked Age-1 Atlantic cod were released in Spring 2003.

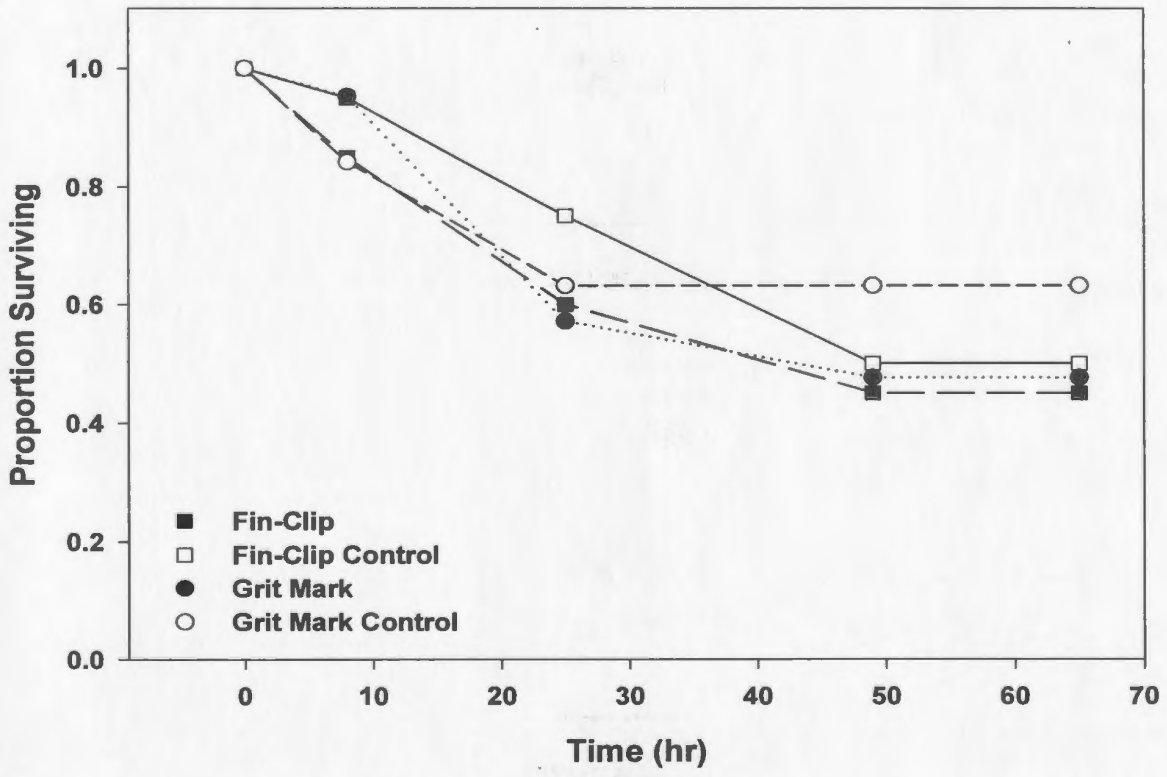

Figure 2.6: The acute mortality assessment for fin-clipped and fluorescent grit marked age -0 Greenland cod (*Gadus ogac*) indicates mortality rates are similar to corresponding control cod.

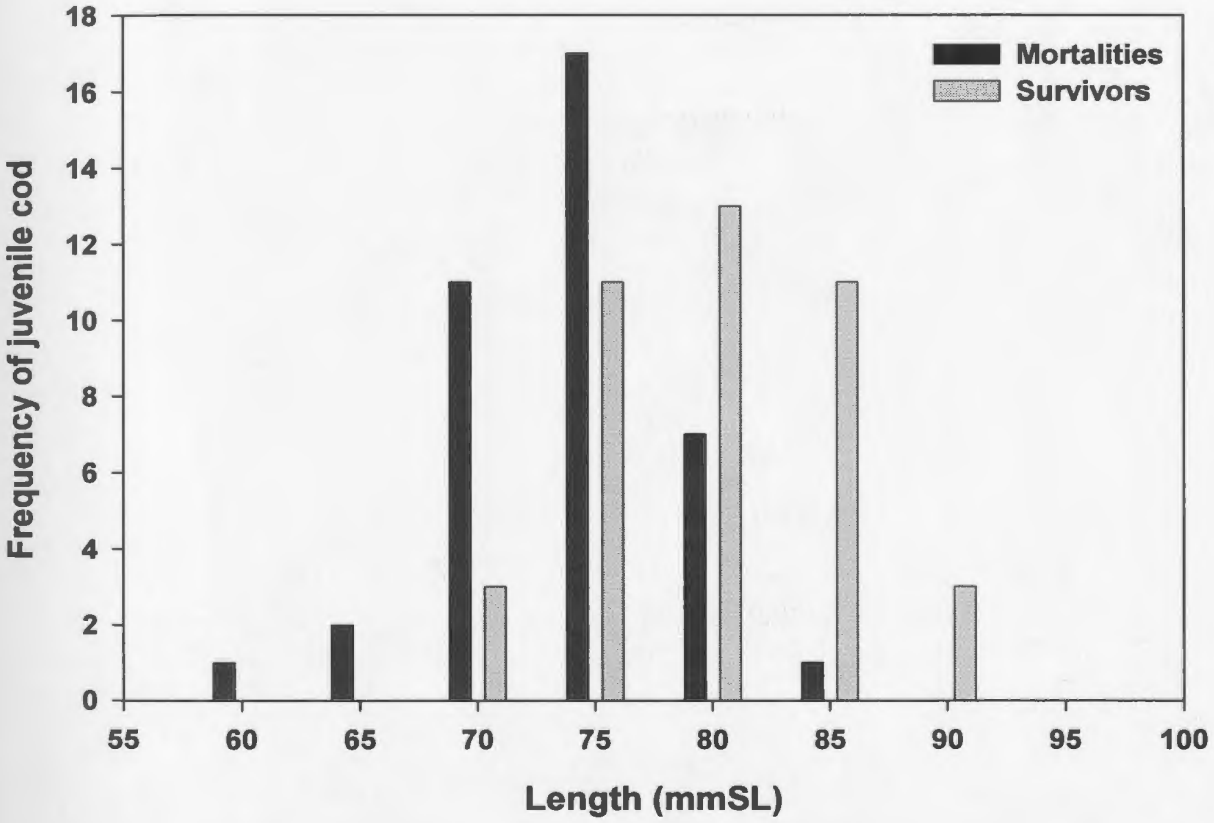

Figure 2.7: Length frequencies of dead and surviving age-0 Greenland cod (*Gadus ogac*) after 65 hours in captivity. The length distributions for mortalities and surviviors were significantly different ($D=0.453$, $p<0.05$), indicating higher mortalities for cod 75 mmSL or less. Length on the x-axis refers to the minimum value of 5 mmSL intervals (i.e., 60 mmSL refers to juvenile cod ranging in length from 60-64 mmSL).

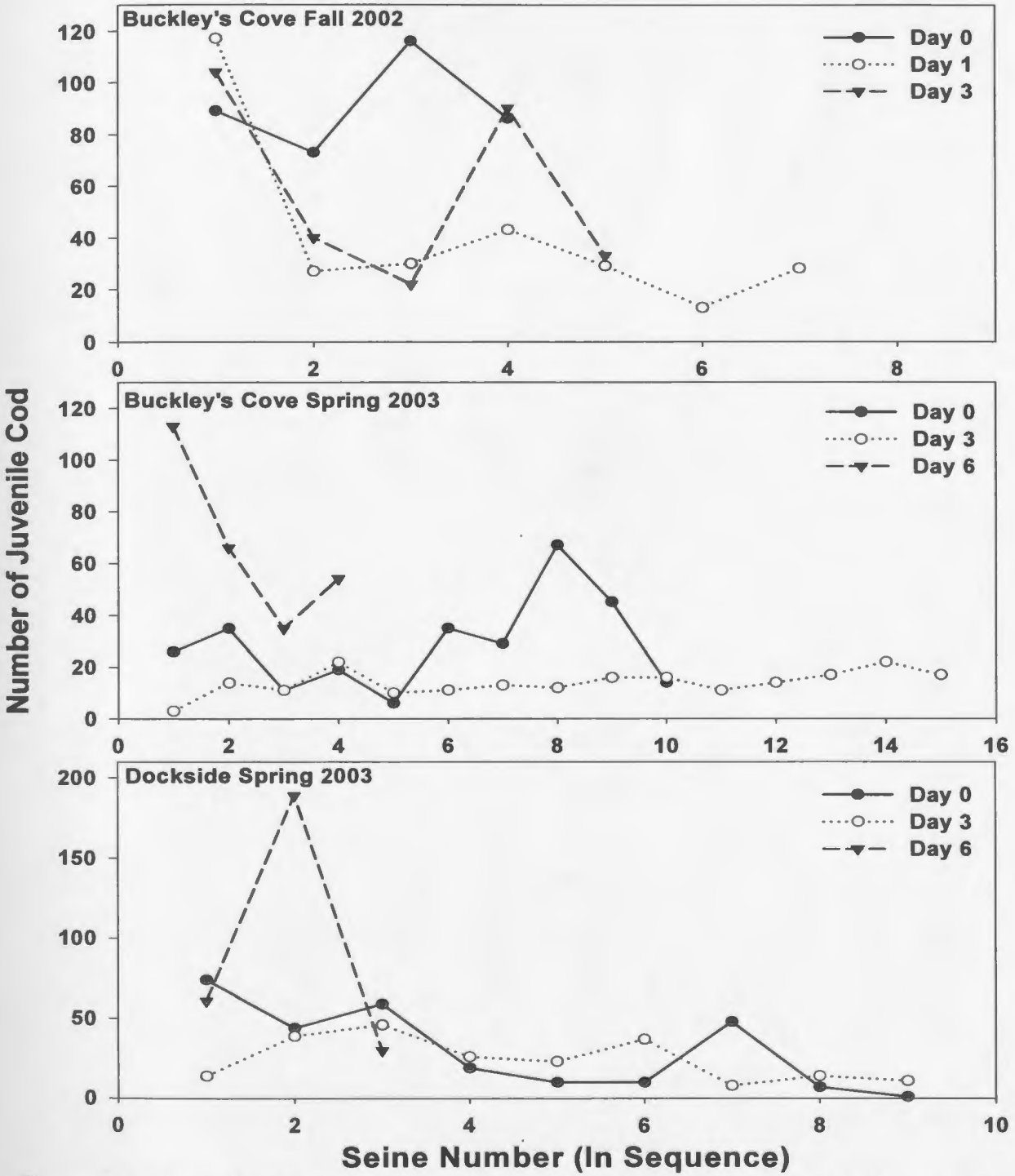

Figure 2.8: Juvenile cod abundances were variable from seine to seine during mark-recapture studies conducted in nearshore Newman Sound during Fall 2002 and Spring 2003. Over a temporal scale of hours, juvenile cod would migrate from areas inaccessible to the sampling gear to areas where capture was possible. The time required to conduct each seine was typically 5-10 minutes.

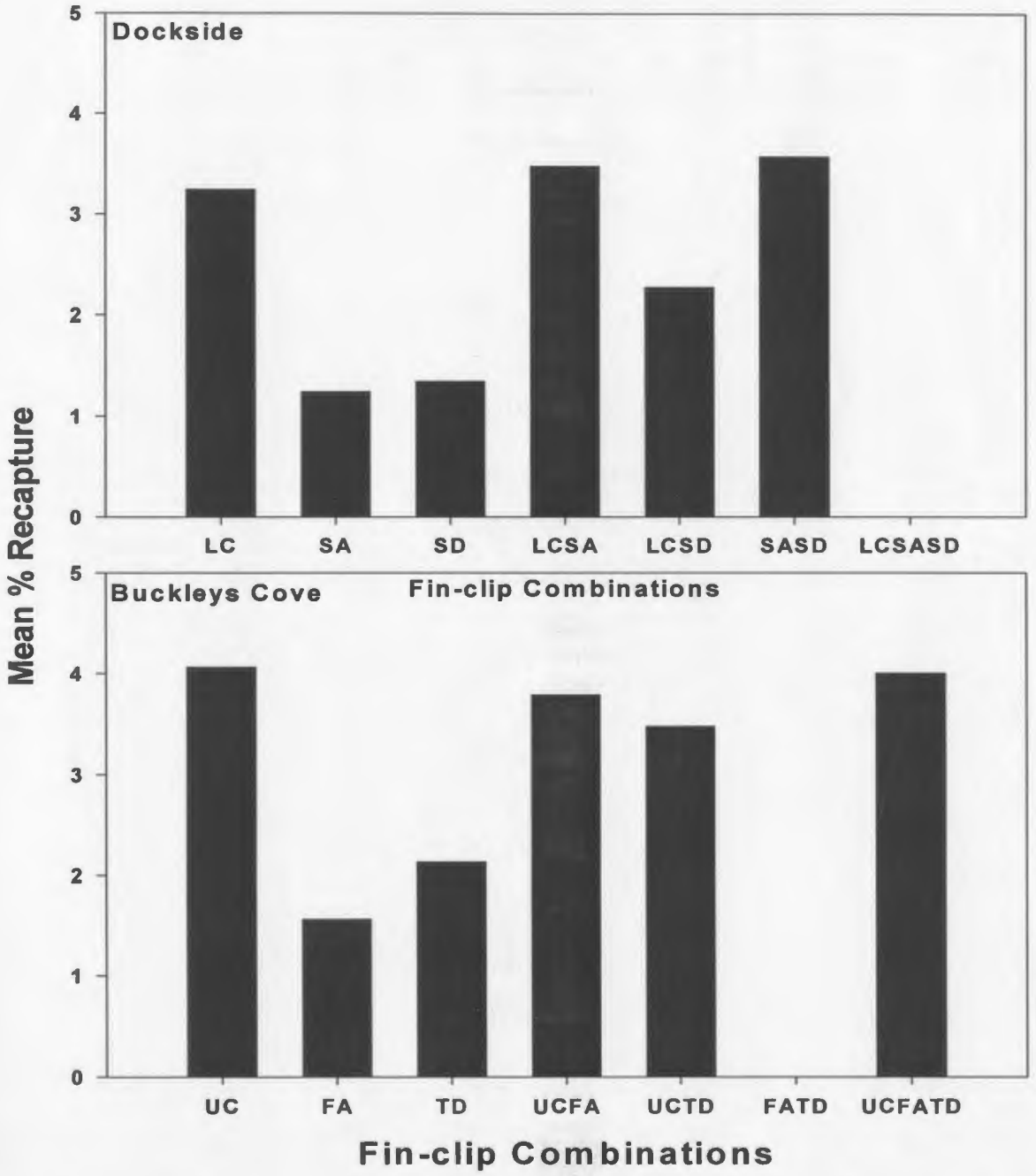

Figure 2.9: The mean percent recapture of the various fin-clip combinations applied to age-1 Atlantic cod at Dockside and Buckley's Cove during Spring 2003. Percent recapture of fin-clips was determined as the number of cod recaptured possessing a particular fin-clip combination divided by the abundance of cod that were released with a particular fin-clip and multiplied by 100. Percent recaptures were averaged over the time period (days) the fin-clips were at liberty. LC = lower caudal; SA = second anal; SD = second dorsal; UC = upper caudal; FA = first anal; TD = third dorsal.

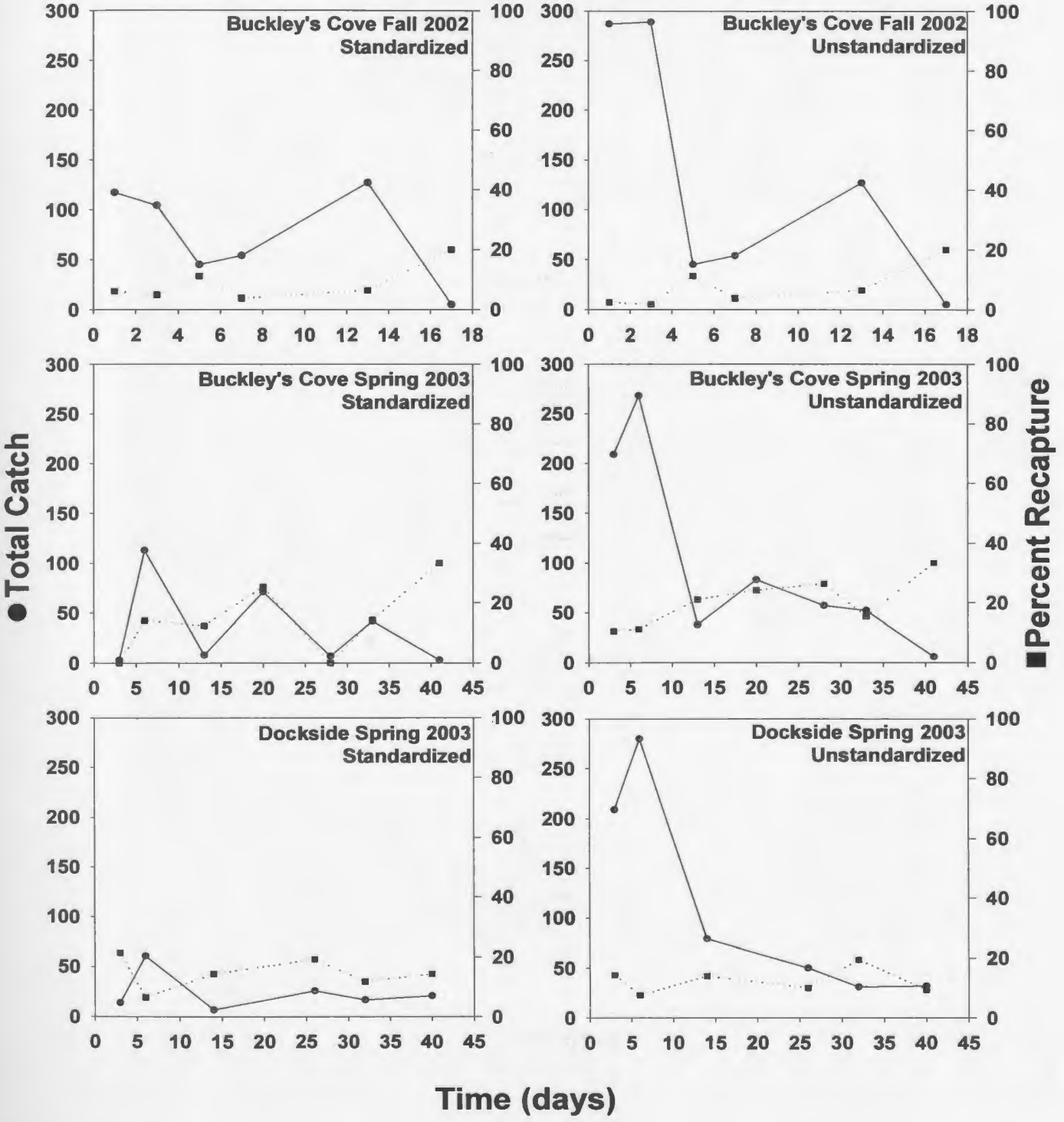

Figure 2.10: The percent of fin-clipped cod recaptured (black squares) remained fairly constant despite cod abundance (black circles) varying from one seine to the next. Similar trends in percent recapture were observed regardless if data were standardized (i.e., only cod from first seine plotted) or unstandardized (i.e.,all cod collected irrespective of differing effort).

Table 2.1: A summary table of marking information for juvenile cod fin-clipped in Newman Sound during 2002 and 2003. Mean lengths (mmSL) pertain to subsampled cod with the number measured in parentheses.

Date	Site	Species	Marking Event	Fin Clipped	Number of Cod Marked	Mean Length mmSL (n)	SD
Oct. 3, 2002 (Day 0)	Buckley's Cove	Greenland cod	M1	Upper Caudal	331	90.7 (33)	5.8
Oct. 4, 2002 (Day 1)	Buckley's Cove	Greenland cod	M2	First Anal	197	95.0 (89)	5.6
Oct. 6, 2002 (Day 3)	Buckley's Cove	Greenland cod	M3	Left Pelvic	290	96.1 (104)	5.4
June 6, 2003 (Day 0)	Buckley's Cove	Atlantic cod	M1	Upper Caudal	236	85.2 (41)	14.5
June 9, 2003 (Day 3)	Buckley's Cove	Atlantic cod	M2	First Anal	206	86.9 (39)	14.4
June 12, 2003 (Day 6)	Buckley's Cove	Atlantic cod	M3	Third Dorsal	246	91.7 (25)	11.8
June 7, 2003 (Day 0)	Dockside	Atlantic cod	M1	Lower Caudal	271	79.6 (31)	13.4
June 10, 2003 (Day 3)	Dockside	Atlantic cod	M2	Second Anal	209	84.0 (20)	11.3
June 13, 2003 (Day 6)	Dockside	Atlantic cod	M3	Second Dorsal	280	79.0 (29)	12.6

Table 2.2: The Kolmogorov-Smirnov test results comparing the length frequency distribution of subsampled cod and cod recaptured on the subsequent sampling day. Significant differences are represented in bold underlined lettering. All distributions became non-significant when lengths were adjusted for daily growth (0.685 mmSLday^{-1}; D. Ings, Department of Biology, Memorial University personal communication).

					Growth Adjusted	
Site	Subsample Collection Day	Recapture Collection Day	D	p	D	p
Buckley's Cove	0	3	0.314	>0.05	0.217	>0.05
Buckley's Cove	3	6	0.174	>0.05	0.149	>0.05
Buckley's Cove	6	13	0.291	>0.05	0.356	>0.05
Dockside	0	3	0.525	**<0.05**	0.092	>0.05
Dockside	3	6	0.238	>0.05	0.15	>0.05
Dockside	6	14	0.261	>0.05	0.392	>0.05

Table 2.3: The age (days) and natural mortality rates (M; day^{-1}) reported in the literature for the egg, larval, juvenile, and adult stages of Atlantic cod (*Gadus morhua*).

Stage	Age (days)	M (day^{-1})	Source
egg	3	0.075	Wieland et al. 2000
egg	6	0.489	Wieland et al. 2000
egg	11	0.296	Wieland et al. 2000
egg	14	0.090	Fossum 1988
egg	15	0.190	Kristiansen et al. 1997
egg	16	0.270	Campana et al. 1989
egg	16	0.140	Campana et al. 1989
egg	16	0.245	Heessen and Rijnsdorp 1989
egg	16	0.215	Heessen and Rijnsdorp 1989
egg	17	0.511	Wieland et al. 2000
egg	17	0.411	Heessen and Rijnsdorp 1989
egg	17	0.277	Heessen and Rijnsdorp 1989
egg	18	0.027	Heessen and Rijnsdorp 1989
egg	18	0.297	Heessen and Rijnsdorp 1989
egg	19	0.110	Fossum 1988
egg	20	0.223	Serchuk et al. 1997
egg	21	0.141	Heessen and Rijnsdorp 1989
egg	22	0.549	Wieland et al. 2000
egg	36	0.150	Campana et al. 1989
larvae	20	0.111	Anderson et al. 1995
larvae	23	0.260	Kristiansen et al. 1997
larvae	23	0.150	Fossum 1988
larvae	27	0.180	Fossum 1988
larvae	33	0.070	Kristiansen et al. 1997
larvae	35	0.046	Blom et al. 1994
larvae	35	0.150	Fossum 1988
larvae	36	0.035	Blom et al. 1994
larvae	50	0.140	Fossum 1988

Table 2.3 (cont.): The age (days) and natural mortality rates (M; day^{-1}) reported in the literature for the egg, larval, juvenile, and adult stages of Atlantic cod (*Gadus morhua*).

Stage	Age (days)	M (day^{-1})	Source
larvae	60	0.031	Blom et al. 1994
larvae	64	0.112	Anderson and Rose 2001
larvae	69	0.084	Anderson and Rose 2001
larvae	71	0.046	Blom et al. 1994
larvae	81	0.068	Anderson et al. 2001
juvenile	100	0.475	Serchuk et al. 1997
juvenile	183	0.010	Julliard et al. 2001
juvenile	183	0.108	Sundby et al. 1989
juvenile	365	0.040	Sundby et al. 1989
juvenile	548	0.0056	Kristiansen et al. 2000
juvenile	548	0.0014	Julliard et al. 2001
juvenile	548	0.0056	Ottera et al. 1999
juvenile	548	0.0057	Ottera et al. 1999
juvenile	548	0.0030	Larsen and Pedersen 2002
juvenile	730	0.00019	Kristiansen et al. 2000
juvenile	913	0.00071	Pedersen and Pope 2003
juvenile	913	0.0014	Larsen and Pedersen 2002
juvenile	1004	0.0048	Anderson and Gregory 2000
juvenile	1095	0.0012	Sundby et al. 1989
juvenile	1278	0.00041	Myers and Doyle 1983
juvenile	1278	0.00056	Myers and Doyle 1983
juvenile	1278	0.00021	Myers and Doyle 1983
juvenile	1278	0.00055	Beverton 1964
adult	2373	0.00069	Beverton et al. 1994
adult	2555	0.000493	Pinhorn 1975
adult	2738	0.00047	Beverton et al. 1994
adult	2738	0.0011	Sinclair 2001
adult	3103	0.00041	Beverton et al. 1994

Table 2.4: Chi-square goodness-of-fit tests computed with program JOLLY comparing the validity of several Jolly-Seber models for mark-recapture data analysis. A significant chi-square result indicates the first model is rejected when compared to the second model (e.g., D vs. A for pooled dataset). P-values equal to 1 indicate insufficient data to perform the test.

Data Set	Models	D vs. A	B vs. A	D vs. B
Buckley's Cove Fall 2002	χ^2	4.1266	0.6055	2.6046
	df	2	0	0
	p-value	0.127	1	1
Buckley's Cove Spring 2003	χ^2	22.6918	0	0
	df	3	0	0
	p-value	<0.0001	1	1
Dockside Spring 2003	χ^2	6.0586	1.9103	4.6069
	df	3	1	2
	p-value	0.1088	0.1669	0.0999
Dockside and Buckley's Cove Spring 2003 (pooled)	χ^2	20.115	4.7447	15.2677
	df	3	1	2
	p-value	0.0002	0.0294	0.0005

Table 2.5: Summary table for various Model A population parameters computed with program JOLLY for juvenile Atlantic cod fin-clipped at Buckley's Cove and Dockside (pooled data). X_t denotes the population parameter in question. $SE(X_t)$ is the standard error including only sampling variance; $SE'(X_t)$ includes both sampling and non-sampling variance. $COV(X_{i,i-1})$ is the estimator covariance.

Parameter	Period	Xt	SE(Xt)	SE'(Xt)	95% C.I.	COV(Xi,i-1)
	1	1.3169	0.31	0.3113	0.7094-1.9245	
Φt	2	0.3783	0.1658	0.1651	0.0533-0.7032	-0.018033
	MEAN	0.8476	0.1479	0.1484	0.5577-1.1375	
	1	1.0961	0.086		0.9275-1.2647	
$\Phi t \Delta t^{-1}$	2	0.7232	0.1057		0.5161-0.9303	-0.003188
	MEAN	0.9097	0.0552		0.8015-1.0178	
	2	667.68		157.83	358.33-977.03	
Mt	3	399		163.09	79.34-718.66	
	MEAN	533.34		113.48	310.92-755.76	
	2	5480.02	1463.8	1436.8	2611.0-8349.06	
Nt	3	3893.94	1658.29	1658	643.70-7144.18	
	MEAN	4686.98	1105.77	1105.85	2519.7-6854.29	
	2	0.0779	0.021		0.0367-0.1190	
pt	3	0.1328	0.0556		0.0239-0.2418	
	MEAN	0.1054	0.0594		0.0164-0.2493	
Bt	2	1828.19	927.33		10.61-3645.76	

Table 2.6: The abundance of the various fin-clip combinations released at Buckley's Cove and Dockside during Fall 2003. UC = upper caudal fin; FA= first anal fin; TD=third dorsal fin; LC=lower caudal fin; SA=second anal fin; SD=second dorsal fin.

Buckley's Cove Fin-Clip Combinations							
Day	UC	FA	TD	UCFA	UCTD	FATD	UCFATD
0	236	0	0	0	0	0	0
3	214	184	0	22	0	0	0
6	191	180	206	17	23	4	5
Dockside Fin-Clip Combinations							
Day	LC	SA	SD	LCSA	LCSD	SASD	LCSASD
0	271	0	0	0	0	0	0
3	241	179	0	30	0	0	0
6	230	172	259	27	11	7	3

Chapter 3: Movement, mortality, and growth of individually tagged age-0 Greenland cod (*Gadus ogac*) in coastal Newfoundland eelgrass habitat.

3.1 Introduction

Greenland cod (*Gadus ogac*) is a member of coastal fish communities of the northwest Atlantic. Its distribution ranges from Baffin Island to Nova Scotia and extends from the intertidal zone to the continental shelf (Scott and Scott 1988). In shallow coastal waters of Newfoundland, abundances of post-settled juvenile Greenland cod are consistently higher in structurally complex habitats (e.g., eelgrass *Zostera marina*) than in structurally simple habitats, such as mud and sand (Laurel et al. 2003b). Fish species, such as Greenland cod, often use complex structure as refuges to reduce predation risk and to optimize growth (e.g., Gotceitas and Colgan 1989; Gotceitas and Brown 1993). In eelgrass, the ability of predators to forage is reduced, and hence, the chance of encountering and capturing prey is lower (Gotceitas et al. 1997). In structurally simple habitats, the foraging ability of predators is not impeded and such areas are risky for juvenile cod to occupy without using predator evasion tactics, such as aggregatory behaviour (Laurel et al. 2004). Association with nearshore habitat is frequently reported to increase the survival of juvenile gadids (Gotceitas and Brown 1993; Linehan et al. 2001; Laurel et al. 2003 a,b), including Greenland cod; however, no studies have attempted to quantify their natural mortality rates within such habitat.

Many fishes experience size-dependent natural mortality rates over their life histories (Sogard 1997). Mortality is inversely associated with age and body size (Peterson and Wroblewski 1984), with the early stages, namely the eggs and larvae, typically exhibiting far higher rates than older juveniles and adults. Presumably to

increase the likelihood that some offspring will reach age-of-maturity (age 3+), Greenland cod have evolved life history strategies whereby vast numbers of eggs are produced and released. Mature adults spawn in the spring (Mikhail and Welch 1989; Morin et al. 1991) and deposit demersal eggs (Methven et al. 2001). Hatched pelagic larvae eventually develop into benthic juveniles that recruit to coastal nursery habitats (Mikhail and Welch 1989; Morin et al. 1992; Methven et al. 2001; Ings 2005) during the summer. Predation is a major source of natural mortality for fish species, particularly the juvenile stages (Lima and Dill 1989; Sogard 1997). When occupying nearshore habitats, age-0 Greenland are prone to a wide array of potential invertebrate, avian, mammalian, and piscine predators. In Newman Sound, tethering studies have identified major fish predators as white hake *Urophycis tenuis*, sculpin *Myoxocephalus* spp., cunner *Tautogolabrus adspersus*, Atlantic cod *G. morhua*, and older conspecifics (Linehan et al. 2001; Laurel et al. 2003a; Gorman 2004). Gape size restrictions typically require piscivorous fish to be twice the body length of prey (Miller et al. 1988), therefore, vulnerability to predation is likely diminished for juvenile fish with high growth rates (see review by Werner and Gilliam 1984). Juvenile Atlantic cod have been observed to have higher growth rates in eelgrass habitat compared to other habitats (Tupper and Boutilier 1995) because of increased food availability (Renkawitz 2004). Juvenile Greenland cod may inhabit eelgrass in coastal Newfoundland in order to optimize the mortality-growth ratio (i.e., optimal foraging theory; Werner and Gillam 1984).

The movements of the species investigated may bias observed mortality rate estimates when conducting survival studies. Some animals that disappear may have

merely vacated the study area, a situation resulting in underestimation of survival. Schneider et al. (1999) confirmed the importance of spatial and temporal scale by showing that movement was of greater importance than mortality at fine scales (<1000 m, <100 d), whereas the opposite occurred at coarser scales. Over the course of their life histories, fish species exhibit varying movement and migratory habits (e.g., Schneider et al. 1999) that result from ontogenetic shifts in diet and habitat association. Larger Greenland cod juveniles (age 1-2) and adults (age 3+) have been described as non-migratory, non-schooling, sedentary fish (Mikhail and Welch 1989; Morin et al. 1991; Nielsen and Andersen 2001). In western Hudson Bay, adult Greenland cod are thought to remain in home inlets for their entire lives and not venture more than a few kilometres (Mikhail and Welch 1989). Age-0 Greenland cod may exhibit higher movement rates than older age-classes. In Newman Sound, Newfoundland, age-0 Greenland cod were observed to exhibit low site fidelity and moved between sampling locations separated by thousands of metres during years of high cod abundance (Laurel et al. 2004). When cod densities are comparatively low in Newman Sound, age-0 Greenland cod appear site-attached, rarely venturing beyond a few hundred metres alongshore (see Chapter 2). Density-dependent movement rates for age-0 Greenland cod necessitates an estimate of movement in order to evaluate survival.

Mark-recapture methodology is routinely utilized to determine key demographic variables, such as population size, growth, survival, and migration, for terrestrial and aquatic species (McFarlane et al. 1990). However, many of the tagging techniques available are more suited for larger, older specimens than for smaller and(or) younger

individuals. When conducting studies on species with small body size or the juveniles of a species, the marking method, soft visible implant (VIalpha™; Northwest Marine Technology Inc., Shaw Island WA, USA) alphanumeric tagging has been used successfully with juvenile Atlantic cod (Olsen et al. 2004). To date, this technique has not been used with juvenile Greenland cod. The minute (1.0 x 2.5 mm), fluorescent tags are subdermally implanted beneath transparent tissue and are externally visible, without the use of expensive equipment, allowing recaptured specimens to be individually identified and released (Rikardsen 2000; Rikardsen et al. 2002). This is in contrast to some internal tags (e.g., coded wire tags) that require the individual to be killed (Isely and Stockett 2001). Individuals can be recaptured multiple times, offering better insight into movement patterns, growth rates (Olsen et al. 2004), and mortality rates (Lebreton et al. 1992). Furthermore, internal placement minimizes the possibility of tag entanglement in complex environments, such as seagrass, macroalgae, or dense undergrowth (Moring 1990), and diminishes the onset of secondary infections and injuries induced by tag movement (Mourning et al. 1994).

If no published accounts are available, experimentation must be conducted to assess tag retention (Shepard et al. 1996), tag visibility, and survival of tagged individuals before the tags are used. Some species have a minimum body size at which tags are sufficiently retained and visible for short-term (i.e., days, months) or long-term (i.e., years) mark-recapture studies. Northwest Marine Technology, the tag producer, recommends individuals be at least 150 mm, based on the studies of Rikardsen (2000) and Rikardsen et al. (2002), to ensure high tag retention and low tagging mortality. Some studies have

proposed smaller length limits (50mm, Griffiths 2002; 140mm, Olsen et al. 2004), though tagging success may be highly species specific. Other species may lack a sufficient amount of transparent external tissue for implantation (Haw et al. 1990). Despite the tag's limitations, it may be appropriate for mark-recapture studies on juvenile Greenland cod.

The main objective of this study was to determine the movement, survival, and growth of age-0 Greenland cod in several eelgrass sites in Newman Sound, Newfoundland, using mark-recapture experimentation. Prior to field studies, I conducted laboratory studies to determine the tag retention, tag visibility, and survival of young-of-the-year Greenland cod inserted with soft VIalpha tags.

3.2 Methods

3.2.1 Study area

I conducted a mark-recapture experiment with age-0 Greenland cod during September-October, 2003, in Newman Sound (48°35'N, 53°55'W; Figure 3.1). The fjord (41 km x 1.5-3.0 km) is situated in Bonavista Bay on the northeast coast of Newfoundland and is divided into two basins, the inner sound and the outer sound. The basins are separated by a sill that rises to an 18 m depth, located approximately 7 km from the head of the sound. The inner sound is shallow (~55 m maximum depth) relative to the outer sound (max >300 m deep). The coastline consists of moderately exposed rocky shores interspersed with sandy coves (pocket beaches). Nearshore substrate varies throughout the sound and ranges from mud to bedrock. Macroalgae (*Laminaria digitata*, *Agarum cribrosum*, *Chondrus crispus*, *Fucus vesiculosus*, and *Ascophyllum nodosum*) and eelgrass are the dominant vegetative cover, with the latter found predominately, where present, in

the subtidal region to a depth of 6 m.

Three major marking sites within the sound were used for the mark-recapture studies. I marked age-0 Greenland cod at two inner sound sites - Dockside (48°33.772'N, 53°57.747'W) and Buckley's Cove (48°35.406'N, 53°54.901'W) - and one outer sound site - Boulder Beach (48°33.714'N, 53°53.326'W). I chose Dockside and Buckley's Cove because they were known from ongoing bi-weekly seining data to be locations of high juvenile cod abundances (Gregory et al. 2002, 2003, 2005). Boulder Beach was located within 236 m of Heffern's Cove (48°33.661'N, 53°53.501'W), a bi-weekly seining site. Exploratory sampling at Boulder Beach indicated high juvenile cod abundances similar to that at Heffern's Cove. All three sites had eelgrass, mud-sand bottoms, and gently sloping bathymetric relief. The major difference among the sites is that the shoreline at Dockside is a long strip of unconvoluted beach whereas Buckley's Cove and Boulder Beach are more sheltered coves. Eelgrass at the three sites consist of extensive meadows interspersed with patches of bare substrate (i.e., mud, sand, gravel). Dockside was adjacent to Headquarters Wharf; Buckley's Cove and Boulder Beach were completely undeveloped. Each marking site was flanked by two adjacent sites ("monitoring sites") located within a few hundred metres that were used to monitor short range juvenile cod movement. The monitoring sites (linear distance from the marking site in parentheses) were Stairs Beach (248 m; 48°33.655'N, 53°57.845'W) and Whiterock (166 m; 48°33.772'N, 53°57.704'W) for Dockside; the sites for Buckley's Cove were Mistaken Cove (162 m; 48°35.347'N, 53°54.999'W) and Pipers Cove (280 m; 48°35.345'N, 53°54.692'W). The sites for Boulder Beach were Heffern's Cove (236 m) and Otter Cove

(83 m). A wharf located between Dockside and Stairs Beach may act as a barrier to juvenile cod along-shore movement. During September-October, 2003, I used VIalpha tagging to mark age-0 Greenland cod at the three main marking locations.

3.2.2 Collection of juvenile cod by beach seining

I collected juvenile cod for marking and tagging studies using a beach seine (Lear et al. 1980; Methven and Schneider 1998). The gear used was a 25 m modified Danish beach seine with a 19 mm stretch mesh, a 24.4 m headrope, and a 26.2 m footrope. Each wing had 75 cm aluminum spreading bars that were 25 mm in diameter. The seine was deployed from a 6 m boat at a distance of 55 m from shore, and retrieved by two people standing 16 m apart on shore. The area sampled was approximately 880 m^2. Chain link on the footrope and a reduced number of floats on the headrope allowed the net to be dragged along the bottom and sample 2 m up into the water column. All fish collected were put into fish tubs filled with seawater, identified, and separated into two groups: age-0 Greenland cod and non-age-0 Greenland cod. The two groups were kept in separate tubs until all seining was completed. Fresh seawater was regularly added to the tubs to replenish dissolved oxygen. Cod were identified to age class, based on age-length values given in Gregory et al. 2002: age-0: $\leq$ 100 mm standard length (SL), age-1: 100 – 200 mmSL, age-2: 200-300 cmSL, and age 3+: >300 mmSL. After juvenile cod were collected for tagging, the other species were released at the capture site.

3.2.3 Soft visible implant alphanumeric (VIalpha) tagging of age-0 Greenland cod

The VIalpha technique involved the insertion of small (1.0 x 2.5 mm), rectangular tags beneath transparent tissue with a modified syringe injector. Each fluorescent tag was

individually labelled with a unique three digit code composed of one letter and two numbers. The implant procedure started with the transfer of one cod to the anaesthetic bath via dip net. When loss of equilibrium in the fish was apparent, I transferred the cod to a moistened measuring board. The tag was implanted beneath the transparent tissue located below the left eye on all individuals. Length was determined to the nearest mmSL and recorded along with the tag code. Prior to measurement, tag visibility and tissue integrity were assessed. Successful tag implantation required all three digits of the code to be visible and that the size of the entry wound be minimal. Mis-marked cod were killed. To determine the rate of tag loss I partially clipped the upper caudal lobe. Double-marked cod were then placed in the recovery bucket containing well-oxygenated seawater. Fully recovered cod were transferred to nearshore holding containers. Total time to process a single cod from the anaesthetic stage to placement in the recovery stage was one minute. Once all cod had been tagged, noticeably stressed or dead cod were removed prior to mass release of healthy individuals. I tagged all released cod along with one other trained person.

Two marking experiments were conducted at Boulder Beach with 106 (85.2±4.7 mmSL) and 308 (84.1±4.3 mmSL) tagged juveniles released on September 29 and October 2, 2003, respectively. Despite an intensive collection effort (> 10 seines), catches of age-0 Greenland cod were extremely low at Dockside and Buckley's Cove. During three marking experiments at Dockside, 101 (88.8±4.8 mmSL), 8 (89.0±4.5 mmSL), and 7 (91.0±3.0 mmSL) cod were tagged and released on October 1, 4, and 9, respectively. Five marking events were performed at Buckley's Cove, which resulted in 30 (88.8±8.2

mmSL), 24 (88.9±5.6 mmSL), 93 (88.8±4.6 mmSL), 72 (91.1±4.3 mmSL), and 16 (99.6±4.2 mmSL) tagged juveniles released on Sept. 30, Oct. 4, 8, 15 and 21, respectively. Monitor seining occurred at each site during every marking event subsequent to the first marking event. I concluded all monitor seining on October 31, 2003. Summaries of the marking data and sampling intensity are presented in Appendix 5 (Table A8) and Appendix 6 (Tables A9-A11), respectively.

A bi-weekly seasonal seining program that was initiated in 1996 (Gregory et al. 2002) commenced on May 27, 2003 and ended November 23, 2003. Sampling consisted of pulling one beach seine haul at each of 12 sites in Newman Sound (Figure 3.1) at low tide (± 2 hours). Collected specimens were enumerated, measured, and then released at the site of capture. Five of the nine sites involved in the mark-recapture study - Dockside, Whiterock, Mistaken Cove, Buckley's Cove, and Heffern's Cove - were part of the bi-weekly program.

3.2.4 Estimation of mortality, growth, and movement of age-0 Greenland cod

Low sample size of recaptured juvenile Greenland cod prevented the determination of survival, and hence mortality, with mark-recapture formulae such as the Jolly-Seber method (see Chapter 2). Instead, I estimated mortality by regressing ln-transformed recaptures against sampling time (days). True mortality rates could not be estimated solely with this method because losses can be caused not only by various sources of mortality (e.g., natural, fishing, tagging, and handling) but also by migration. If mortality rates at a given size are constant with time, as indicated by the goodness-of-fit, the slope of the line produces an estimate of apparent total mortality (Z) (Kristiansen et al. 2000);

however, in this study, fishing mortality was nil, and Z therefore approximates the instantaneous natural mortality rate (M) assuming tagging/handling mortality and migration losses are not substantial. If migration and tagging/handling mortality can be estimated, then the apparent M can be adjusted to reflect better the true M. I used this method by incorporating all recaptures collected in the outer sound, but a poor model fit suggested that the assumption of constant temporal mortality rates was violated. Instead, only recaptures netted at the marking site, Boulder Beach, were used. Although tagging mortality was negligible, tank studies indicated that handling mortality may have approached nearly 20% (see Section 3.3.5). A rough measure of minimal migration from the marking site was estimated using the following equation:

$$\%m = 100[R_{AS}/(R_{AS} + R_{MS})] \quad (3.1)$$

where %m is the minimal percent migration from the marking site, R_{AS} is the number of recaptures collected at the adjacent monitoring sites over the duration of the entire study, and R_{MS} is the number of recaptures captured at the marking site over the duration of the entire study.

I estimated individual specific growth rates (SGR; $\%day^{-1}$) for tagged cod in tank and field studies with the equation used by Olsen et al (2004):

$$SGR = 100[\ln(L_2) - \ln(L_1)]/(t_2 - t_1) \quad (3.2)$$

where L_2 and L_1 symbolize the standard lengths (mm) of individuals examined (or sampled) during sample time (t_2) and the previous sample time (t_1). The mean SGRs were calculated for both tank controls and age-0 Greenland cod netted at Heffern's Cove for each bi-weekly sampling date. Linear regressions were performed to determine if SGR

was related to initial length at tagging for tank cod (T_{SGR} = tank cod SGR, T_{LENGTH} = tank cod initial length) and field cod (F_{SGR} = field cod SGR, F_{LENGTH} = field cod initial length). In addition, an ANCOVA was performed to determine if the relationship of SGR and initial tagging length differed between the two treatments.

3.2.5 Determination of tag retention, tag visibility, and survival of VIalpha tagged cod

Preliminary studies were required to determine tag retention, tag visibility, and survival of VIalpha tagged cod. From May 19-June 1, 2003, I used a tank study to compare the tag retention and survival of tagged and untagged (control) cod. Age-0 Greenland cod were not available at the time of the tank study; age-0 Atlantic cod were therefore used instead. Age-0 Atlantic cod were reared at the Ocean Science Centre, Logy Bay, Newfoundland, from Placentia Bay broodstock. Juveniles were raised from eggs hatched at the facility and were initially given live feed (algae, rotifers, *Artemia*), then switched to dry feed at 50-60 days old (Boyce 2003, personal communication). Photoperiod was 24 hours/day with a light intensity of ca.100 lux. Mean water temperature was 11.0˚C.

When cod were 50-60 mmSL (~90 days old), I transferred 100 individuals to a fibreglass holding tank (1.0 m^2 x 0.5 m) on May 19, 2003. Cod were allowed to acclimate to tank conditions for three days before tagging commenced. On May 22, ten cod at a time were transferred from the holding tank to a 20-L bucket. Cod were individually anaesthetized to a state of complete loss of equilibrium and reduced operculum movement with a 40 mg clove oil/L and 400 µL/L ethanol mixture added to 5 L of seawater. Cod were then transferred to a Petri dish partially filled with seawater for tag injection. I

inserted an orange VIalpha tag beneath the transparent skin located below the left eye with an injector sterilized with ethanol. Length was recorded to the nearest mmSL. Tagged cod were transferred to a 20 L recovery bucket filled with fresh sea water and oxygenated with a bubbler and airstone. Tearing of the cheek tissue occurred with four of the smaller cod during the injection process. These cod were discarded. Once individuals had completely recovered, they were transferred to a black, mesh-bottom bucket in the holding tank to prevent mixing of tagged and untagged cod. Control cod were subjected to the exact procedures as the tagged cod, with the exception of active tag insertion. Instead, the tag applicator was placed near the site of insertion for 2-3 seconds, the time typically required to inject a tag.

Three adhesives were tested to determine if tag retention could be improved. The adhesives used were Crazy Glue (Elmer's Product Inc., NY, USA), New Skin Antiseptic Liquid Bandage Spray (Medtech, NJ, USA), and Vetbond Skin Adhesive (3M, Toronto, ON, Canada). Using a fine tipped artist brush, I applied the adhesives to the injection wounds of 30 age-0 cod (10 cod/adhesive).

Problems with this procedure immediately became apparent when the majority (>80%) of processed cod did not recover. To determine the cause of the high mortality, steps in the procedure were removed sequentially: (1) morphometric measurements (thereby reducing air exposure); (2) use of adhesive; and, (3) sterilization of the injector. The concentration of the clove oil-ethanol mixture was also varied. None of the changes improved the survival rate of tagged cod. I speculated that the anaesthetic or the small size of the cod may have contributed to the increased mortality. The procedure was

repeated on May 25, 2003, with carbon dioxide (CO_2; concentration = 1.0 gL^{-1}) used as the anaesthetic. This concentration was obtained through dissolution of one 5 g packet of Eno Antacid Effervescent (SmithKline Beecham, ON, Canada) in 5 L of seawater. The steps of measuring length and the use of adhesives were again omitted. Survival improved noticeably (>80%) and the method was adopted.

Cod tagged on May 25, 2003, were examined daily from May 26-June 1, 2003 for tag retention, survival, and visibility of the tag. I removed each cod from the holding tank and examined the site of insertion for tag presence, tag visibility, and presence of injury or secondary infection. The examination process was accomplished within a few seconds and tag visibility was enhanced with the use of a flashlight with blue light emitting diodes (LED) and amber filter glasses. Anaesthetization was required if tags were difficult to read or the cod was overly active. I transferred inspected cod to a mesh-bottom bucket located in the holding tank. Dead fish were removed, measured, and codes recorded. On June 1, the cod were examined, killed, and measured to nearest mmSL. Tags were removed to verify code.

Tag retention was low (<50%) during the tank study. Some tags had been completely shed while others were in the process of being shed. Because of the small size of the cod used, the availability of transparent tissue on the head was limited. Tags barely fit, with the distal edge of the tags located close to the injection wound. Tags may have been lost as a result of body undulations. Tag loss appeared to be reduced with larger body size. An increase in body size was also assumed to reduce the proportion of cod rejected because of tissue tearing. From October 21-November 8, 2003, I conducted a

second tag study at the Marine Interpretation Centre, Terra Nova National Park, Newfoundland, to determine if shedding rates decreased with increased body size.

On October 17, 2003, 62 age-0 Greenland cod were collected and transferred to a 1835 L semi-circular, flow-through (flow rate = 21Lmin^{-1}) holding tank composed of fibreglass and plexiglass at the Marine Interpretation Centre. Cod were acclimatized to tank conditions for four days. On October 21 (Day 0), juvenile cod were individually anaesthetized with CO_2 (1.25gL^{-1}). After inserting the tag beneath the eye, I recorded the length (mmSL) and administered a partial (1/6th) upper caudal fin-clip. Processed fish were then transferred to a 20 L mesh-bottom bucket partially submerged in the holding tank. Control fish were processed in the same manner, except that actual tag insertion was eliminated and the lower caudal lobe was partially clipped instead of the upper caudal fin. Fish that were stressed, injured, or dead were removed and the tag code recorded, if present. Successfully-processed cod were released into the holding tank. In total, 27 tagged cod (94.2±7.8 mmSL) and 23 (96.2±6.3 mmSL) control cod were released.

Tank cod were fed twice a day with minced capelin (*Mallotus villosus*) or occasionally live mysids and amphipods. The tank was inspected daily for mortalities. Every 2-3 days, I examined individuals for tag retention, tag visibility, and stress-related injuries. Most cod could be examined without using the blue light and amber filter glasses. A small portion of cod required anaesthetic because tags were partly obscured. Lengths were measured to nearest mmSL. On November 8 (Day 18), the remaining individuals were killed and preserved in ethanol for microscopic examination of the wound area. The insertion wounds of all tagged fish had healed by Day 18.

After the tank study, a fully factorial two-way analysis of variance (ANOVA) was performed to determine whether mean length differed with treatment (VIalpha tagged cod, control cod), and time (i.e., days after treatment). The significance level (α) was set at 0.05. Non-significant difference in lengths between treatments would rule out differences in tagging mortality rates due to body size.

3.3 Results

3.3.1 VIalpha mark-recapture of age-0 Greenland cod

Despite an intensive sampling effort (>10 seines) at the marking locations, Boulder Beach was the only site where a large number of cod (n = 450) was collected, tagged, and released. The majority of cod tagged at Boulder Beach were collected with a single seine (Figure 3.2). From the releases at Boulder Beach, 18 were recaptured (Table 3.1), resulting in a recapture percentage (R%) of 4%. Of the 18 recaptures, three were recaptured twice, resulting in a multiple-recapture percentage of 17%. One cod was recaptured twice on the same day of sampling; following release at Boulder Beach, it was re-caught 83 m away at Otter Cove, indicating intersite movement was possible in a time span of a few hours. Given that one fin-clipped cod was recaptured without a tag, the tag loss was estimated at 6%, compared to the tank tag loss of 5%. Furthermore, readable tags were readily observed for all recaptured cod.

Recapture percentages for tagged cod at Dockside and Buckley's Cove were relatively low (3% and 1%, respectively). All recaptures (n=5) were made at the site of release, except for one cod at Dockside that was netted twice at Stairs Beach (Table 3.1). Because the number of recaptures were extremely low, results from these sites are not

discussed in further detail.

3.3.2 Movement of age-0 Greenland cod

Intersite movement was prevalent for cod tagged at Boulder Beach and increased over the duration of the mark-recapture program (Figure 3.3). Over the first 15 days of the study, tagged cod were often captured at Boulder Beach, the site of release, with some appearing at Heffern's Cove (a distance of 236 m). After day 15, more juveniles were recaptured at Heffern's Cove (n = 3) than the release site (n = 1). Only one cod was recaptured at Otter Cove and it had previously been recaptured at the release site that same day. Overall, percent migration from the release site was roughly 39% (total number of tagged cod recaptured at the adjacent monitoring sites/total number of tagged cod recaptured in outer Newman Sound = 7/18). Intersite movement was also observed at Dockside, despite the low number of releases (n = 129) and recaptures (n = 2) made there. One cod was released at Dockside and recaptured twice at Stairs Beach, suggesting that the presence of the wharf between these sites did not completely deter along-shore movement. Despite this movement between nearby sampling sites, tagged cod remained at the same general marking location. From Oct. 9 - Nov. 23, 2003, a total of 473 age-0 Greenland cod were collected from 12 sites in Newman Sound that were sampled with a single seine/site every two weeks. No tagged cod were collected during these seines, suggesting that long range along-shore movements (>1000m) to other nearshore sites are rare for this age class. However, the absence of recaptures at distant nearshore sites does not exclude the possibility of extensive movements to offshore waters. No trend was observed between distance travelled and the time tagged cod spent in the wild prior to

recapture (Figure 3.4).

3.3.3 Natural mortality of age-0 Greenland cod

The daily M was estimated as 0.034 day^{-1} for all recaptures in the outer sound (Figure 3.5); however, the fit of the regression line to the data was relatively poor (r^2=0.278). Furthermore, fit of the model proved non-significant ($F_{1,3}$=1.16, p=0.361). Goodness-of-fit greatly improved (r^2=0.915), and the general linear model became significant ($F_{1,2}$=21.39, p=0.044), when only recaptures collected at the marking site, Boulder Beach, were regressed against time; M was estimated at 0.052 day^{-1}. Migration of cod from Boulder Beach to the adjacent monitoring sites was estimated as 39% over a period of 27 days. Handling mortality was estimated as 20% from a preliminary tank study using the percent survival of both tagged (22 surviving tagged cod/27 total tagged cod = 0.82) and control cod (18 surviving control cod /23 total control cod = 0.78). Migration and handling mortality estimates reduced M to 0.021 day^{-1} [= (0.052 day^{-1} - (0.39*0.052 day^{-1} - 0.20*0.052 day^{-1})]. The observed mortality rate would suggest that roughly 880 out of 1000 age-0 Greenland cod survive a one week period.

3.3.4 Specific growth rates of tagged and untagged age-0 Greenland cod

Overall, mean SGR for recaptured cod (Table 3.2; mean = 0.27±0.38%day^{-1}; range = -0.38 to 1.20%day^{-1}) was noticeably lower than the tank cod (mean = 0.38±0.12%day^{-1}; range = 0.00 to 0.60 %day^{-1}); but not significantly so (t = -1.18, p = 0.26, df = 17). Recaptured field cod exhibited a significant trend of decreasing SGR with initial release length (Figure 3.6; $F_{SGR} = 3.52 - 0.037F_{LENGTH}$; F=8.45, df=1, p=0.011) whereas tank cod exhibited a non-significant positive relationship ($T_{SGR} = 0.128 + 0.0027T_{LENGTH}$; F=0.67,

df=1, p=0.42). The relationship between SGR and initial release length was significantly different between the two groups (treatment term: F=11.56, df=1, p=0.002; length term: F=9.68, df=1, p=0.004; interaction term: F=12.95, df=1, p=0.001). Figure 3.7 shows that SGR does not decrease or increase with time since release for tagged cod, and that most cod spent ten days or less post-release prior to recapture (Table 3.2). Two cod were recaptured 26 days after release; one had an above average SGR (0.67%) and the other was below average (0.22%). Six cod did not display any growth and two of these were in the wild for more than one week and presumably had time to recover from the stresses of handling and tagging. The SGR of wild, untagged Greenland cod was estimated from juveniles collected during the bi-weekly sampling program. Newly-recruited juveniles first appear in beach seines at Heffern's Cove on July 31 with a mean SL of 40±6.6 mm. Mean length on the last sampling day, November 23, was 106±6.2 mmSL. Though individual SGRs could not be determined from unmarked fish, mean SGRs were calculated for each sampling period between July 31 to November 23 (Figure 3.7). The overall trend is a decrease in mean SGR with time. The mark-recapture program commenced on September 30 and the individual SGRs for recaptured cod are also plotted in Figure 3.7. All tagged cod, except one, either fall on the line or beneath it, suggesting tagged cod have a lower daily length increase than untagged wild cod; however, this difference was not significant (t=-1.1754, df=18, p=0.255).

3.3.5 VIalpha tag retention and survival tank studies

Preliminary tank studies of VIalpha tagged age-0 Greenland cod indicate that survival and tag retention were high once an appropriate tagging technique was developed.

Earlier attempts at tagging resulted in low survival and retention as a result of small cod size, mortality-inducing collection and transportation stresses, and the use of clove oil as an anesthetic. Tagging mortality may have also been attributed to inexperience with the tagging method. At the conclusion of the third tank study, tag retention was 95% for the 22 surviving tagged cod (101.4±8.8 mmSL). Tag loss was recorded for one cod measuring 85 mmSL on Day 6. Because tag loss was so low, the relationship between retention and cod length could not be determined. Tag visibility was also good and tags were generally readable without the aid of blue light; in only two cod was blue light necessary to identify tags obscured by pigmentation.

The initial mean lengths of tagged and control cod were 94.2±7.8 mmSL (range = 81-107; n=27) and 96.2±6.3 (range = 78-106; n =23), respectively. Throughout the experiment, there was no significant difference between tagged and control cod in terms of length (Table 3.3; $\chi^2 = 5.79$, df = 1, p = 0.061) or length with time ($\chi^2 = 0.77$, df = 6, p = 0.993). The proportion of tagged and control cod surviving over the duration of the tank study was plotted to determine if the mortality rate in tagged cod was higher (Figure 3.8). Survival for control cod was high (~ 96%) for the first 12 days of the experiment with only one individual dying during the first three days. Three tagged experimental cod died over a period of four days (Days 5-8). At the end of the study, tagged cod had similar survival (82%, n = 22) compared to control cod (78%, n =18). Figure 3.8 shows a noticeable increase in mortality on Day 13 for both treatments that was caused by severe fin rot in three control and two tagged cod. These individuals were removed from the tank and recorded as mortalities, though the tag itself was not the direct causative mortality

agent. The mean length of the dead fish (88±7.2 mmSL) was significantly lower when compared to that of all fish on Day 0 (95±7.1 mmSL; $t=3.00$, $p=0.010$, $df=13$) and all survivors on Day 18 (102±8.4 mmSL; $t=5.32$, $p<0.001$, $df=16$). Smaller length may indicate a tank effect or intraspecific competition with larger cod that inflict caudal wounds on smaller conspecifics. Larger cod appeared to dominate food consumption when fed, and smaller cod were often chased away from the food and could not feed until larger individuals reached satiation.

3.4 Discussion

Age-0 Greenland cod exhibit low movement that is limited to migrations of a few hundred metres and individuals remain in close proximity to sites of release. Olsen et al. (2004) observed that VIalpha tagged juvenile Atlantic cod remained at release sites along the Norwegian Skagerrak coast. Grant and Brown (1998) found that age-0 Atlantic cod remained localized in eelgrass habitat at sites on the coast of Newfoundland for several weeks after settlement to the bottom. They also found evidence for overwintering behaviour in these habitats when they captured age-1 cod the following spring that had been initially marked during the previous fall as age-0 cod. Enhancement studies conducted in western Norway have shown that 90% of released juvenile (age 1 and 2) and wild tagged cod were recaptured within 10 km of the release location (Ottera et al. 1999). Skreslet et al. (1999) recaptured 84% of 2-3 year old tagged wild cod within 1 km of the tagging areas in northern Norway. Others were captured within 20 km, though one individual was found 65 km away 470 days post release. Older juvenile and adult Greenland cod are reported to have high site fidelity with no large evidence of long-range

migrations. For example, individuals (75-475 mmTL) in western Hudson Bay did not venture beyond a few kilometres during their lifespans (Mikhail and Welch 1989). After observing low returns of age 1-9 Greenland cod (121-596 mm) tagged in eastern James Bay, Morin et al. (1991) suggested that the species may have a large, or diffuse, home range; however, a low recapture rate may have resulted from the small abundance of tagged cod released, tag losses and(or) tagging mortality.

Juvenile cod undergo diel migrations in nearshore Newfoundland, which may explain the low recapture percentage observed for VIalpha tagged cod in this study. Older juvenile cod (age 1+) move from deeper, cooler water inhabited during the day to shallower, warmer water at night (Keats 1990; Cote et al. 2001). Transitory habitat change is initiated before twilight to decrease predation risk from predominantly visual predators, and to increase food availability (Linehan et al. 2001). When light intensities diminish at dusk, aggregated cod disperse and distribute over the bottom, regardless of substrate or associated vegetation. Reduced light levels lower the foraging efficiency of predominantly visual predators in shallow water. Despite reduced visibility, predator concentration increases in the nearshore because larger piscivorous fishes, such as older conspecifics and Atlantic cod, are not deterred from entering shallow waters where avian predators such as gulls, eagles, and osprey are abundant (Linehan et al. 2001). I observed some evidence of inshore juvenile cod migration while seining for the second marking event (October 2) at Boulder Beach. Repeated sampling attempts at the marking site produced cod abundances that were too low for tagging. Collection was abandoned for several hours so that monitor seining of adjacent sites could be completed. Later, a single

seine pulled at the marking site, approximately an hour before dusk, captured over 300 individuals. Similar abundances were not observed at the adjacent sites, suggesting that the cod had possibly migrated from deeper water or areas inaccessible to the seining gear. It should be noted that observation was based on a single event and must be considered speculative, though similar observations have been reported by other researchers. Morin et al. (1991) observed higher captures of older Greenland cod at night during the day in shallow water; however, juveniles <100mm were never captured in estuaries or along the coast of eastern James Bay near their study site. Whether or not juveniles exhibited similar diel movements remains unknown and requires study in Newfoundland waters. The authors also noted that temperature-dependent seasonal movements occurred. Adult Greenland cod were more abundant in shallow (2-5m) estuarine waters in winter than in summer (Morin et al. 1991). Adults have also been captured in estuaries during the spring with abundances declining in summer, suggesting offshore movements to avoid higher temperatures (Lambert and Dobson 1982). A higher capture percentage might have been achieved in Newfoundland waters if sampling had been conducted at night, instead of solely during the day. Night sampling should be added as a component of any future mark-recapture studies of cod. Also, further study is required to determine the extent of diel migrations to deeper waters by age-0 Greenland cod because mortality rates may be biased if the movements are perceived to be permanent. Apparent mortality estimates group death and emigration as losses to the natural system, with the implication that the observed emigration is permanent. However, Pollock et al. (1990) stated that temporary emigration may be common in many field situations and that the resulting bias may be

serious regarding parameter estimates. The existence of temporary emigration can lead to apparent mortality being overestimated because animals seemingly lost are returning to the system.

The instantaneous natural mortality (M) of 0.021 day^{-1} determined in this study for age-0 Greenland cod, though based on four data points, is comparable to estimates reported from other studies. For 6-12 month old Atlantic coastal cod along the Norwegian Skagerrak shoreline, Julliard et al. (2001) estimated M at 3.8 $year^{-1}$, equivalent to a M of 0.010 day^{-1}. Kristiansen et al. (2000) estimated M at 0.0056 day^{-1} for age-0 Atlantic cod tagged and released at Heimarkspollen, Norway. Although their estimate is nearly four times lower than this study the cod they examined had a mean length of 120 mm, which is slightly larger than the juvenile cod used in this study. The size difference between the studies was slight, however, the larger size may have been sufficient for Heimarkspollen cod have enter a size refuge from most piscivores. Julliard et al. (2001) found that Z dropped dramatically for age-1 coastal cod compared to younger, smaller conspecifics because individuals of the cohort were too large to be preyed efficiently upon by other fish species. At the same time, these individuals were too small to be exploited in commercial and recreational fisheries, and values of Z increased once the cod had recruited to the fishery. The M estimate from this study was higher, as expected, than that reported for larger, older (age 1+ to 3+) northwest (0.0002-0.005 day^{-1}; Beverton 1964; Myers and Doyle 1983; Anderson and Gregory 2000) and northeast Atlantic (0.0007-0.001 day^{-1}; Sundby et al. 1989; Larsen and Pedersen 2002; Pedersen and Pope 2003) juvenile cod. For adult Greenland cod, Mikhail and Welch (1989) used catch curves to estimate

mortality as 0.5 $year^{-1}$, which is roughly equal to $Z = 0.00082\ day^{-1}$. Therefore, even if fishing mortality is assumed absent, the mortality of adult cod is 25 times lower than the mortality of juveniles.

Low recapture abundances at Dockside and Buckley's Cove precluded mortality estimates for cod at those sites, and it is unknown if the mortality rate observed at Boulder Beach is typical. Mortality may be high at Boulder Beach because predation risk may be high. High prey abundance attracts high predator density; increased predation risk may elevate prey mortality despite the presence of complex habitat (Laurel et al. 2003a). In 2003, Hefferns Cove was one of the highest producers of fish abundance in Newman Sound (Gregory et al. 2005), which is similar to observations over the previous seven years (Gregory et al. 2002). Of the 12 sites, Hefferns Cove was frequently the highest producer of juvenile gadoid (Greenland cod, Atlantic cod, white hake *Urophycis tenuis*) abundance and potential predators. Known piscine predators of juvenile cod at this site included older (age-1+ to 3+) conspecifics, sculpins (*Myoxocephalus* spp.), and Atlantic cod (Linehan et al 2001; Laurel et al. 2003a). Mammalian predators, such as otters (*Lutra lutra*; H.Stewart, Department of Biology, Memorial University of Newfoundland, personal communication) and harbour seals (*Phoca vitulina*; Hammill and Stenson 2000), were also observed. Avian predators are also present, including gulls, terns, mergansers, loons, cormorant, eagles, and osprey (Linehan et al. 2001). The presence of potential predators is not sufficient evidence that predation mortality is high for Greenland cod, particularly if predators prefer other available prey items. Greenland cod in Western Hudson Bay co-exist with a number of potential marine mammalian (ringed seal *Phoca hispida*, harbour

seal, beluga whale *Delphinapterus leucas*) and avian (black guillemots, thick-billed murres) predators (Mikhail and Welch 1989); however, gadids were not a major part of their diets. This finding, in combination with the absence of cod in the stomachs of 50 sculpins, led Mikhail and Welch (1989) to conclude that Greenland cod was not a vital intermediary in Arctic food webs. This is in contrast with coastal co-habitants (e.g., Arctic cod *Boreogadus saida*) that play an important role as major prey for whales, seals, birds and charr. It is difficult to determine if Greenland cod in Newman Sound are vital prey for larger species. Tethering studies of juvenile cod predation have often used both Greenland and Atlantic cod juveniles (Linehan et al. 2001; Laurel et al. 2003a; Gorman 2004), because they are similar in morphology (Methven and McGowan 1998) and behaviour while tethered (Laurel et al. 2003a). No studies have determined the gadoid prey preferences of Newman Sound predators.

Little information is available concerning the effect that VIalpha tags have on juvenile cod growth. Olsen et al. (2004) reported that tagged cod grew 0.46% daily under lab conditions; however, similarity to untagged cod was not determined and specific growth rates of recaptured cod were not compared between lab and wild tagged fish. Rikardsen et al. (2002) stated that VIalpha tagged charr grew significantly better than Floy tagged charr and that the former seemed to have no effect on the growth. During my study, the mean SGR for tagged cod was lower than untagged wild cod, but differences were non-significant. Though similar, the SGRs for tagged and untagged wild cod should be treated with caution because size-selective mortality may be negatively affecting small cod and bias the mean values upwards. The small size differences (i.e., millimetres)

observed between sample times for juvenile cod may be concerning because fish lengths recorded with good precision in the field may still involve a small degree of error (Gutreuter and Krzoska 1994). Recently, field workers in Newman Sound, using the measuring boards from my study, demonstrated that measurement error can be very small after five independent observers recorded the lengths of eight juvenile cunners (pooled standard error = 0.16 mmSL; range = 0.20 mmSL to 0.87 mmSL; see Appendix 7 Table A12). The overall percent error, expressed as the ratio of standard error to mean length, was 0.27%, indicating that *in situ* measurement error can be negligible. The relationship between SGR and initial tagging length differed when tank cod were compared to field-released cod. For cod held in tanks, SGR was relatively constant over the lengths examined; however, the SGRs for field cod were negatively correlated with increasing body size. The discrepancy between the growth rates of tank cod and field cod may be attributed to tank effects. During tank studies, larger cod appeared to dominate food consumption when fed, and smaller cod often could not feed until larger individuals reached satiation. In the natural environment, the ability to forage may not be hindered for small cod that require fast growth rates to reach size refuges from potential predators. In addition, higher food densities would be available to field cod inhabiting eelgrass (Renkawitz 2005).

The slightly higher estimate of M relative to previous studies may be attributed to an underestimate of tagging and handling mortality. Tagging mortality was negligible in tank studies; however, indirect tagging-induced mortality may be present. It is unlikely that the tag itself was visually observable to potential predators given its small size and

subdermal implantation (Rikardsen 2000). However, altered behaviour caused by handling stress may be a problem. For instance, once released, tagged cod may swim rapidly away from the point of disturbance, irrespective of the suitability of habitat types. This high activity may increase encounter rates with nearby predators. Furthermore, tag insertion inflicts a small wound near the eye of the cod. Some predators, such as older conspecifics, can track prey using chemosensory cues (Cote et al. 2001) and may detect the presence of tagged cod because of its injury. Linehan et al. (2001) proposed a similar scenario as a caveat of the tethering method where the injury caused by insertion of the hook into the caudal fin may attract a higher density of predators than otherwise present. A better estimate of tagging-related mortality would require the inclusion of known predators in tank studies to compare encounter rates of tagged and untagged individuals. Such a study has not been conducted so it is difficult to determine if VIalpha tagged cod are more prone to predation than untagged conspecifics.

Tag retention was high for VIalpha tagged juvenile Greenland cod in tank and field experiments. Tag retention (95%) in this study was equivalent or higher than that reported for other fishes. Olsen et al. (2004) observed relatively high overall tag loss (33%) after a 150-day tank study for age-0 Atlantic cod (*G. morhua*), with the majority of losses occurring between weeks 1 and 9. Hatchery rainbow trout (*Oncorhynchus mykiss*) exhibited a mean retention of 83% over a period of 25 days (Isely et al. 2004), although the VIalpha tags used were slightly larger (1.5 mm x 3.5 mm) than this and most other studies. Recaptured lake-dwelling and sea-run smolts of Arctic charr (*Salvelinus alpinus*) demonstrated strong size-dependent tag retention, ranging from 46-68% for individuals

less than 150 mm and ranging from 91-100% for individuals greater than 150 mm (Rikardson 2000). Rikardson et al. (2002) also reported tag retention of 78% for hatchery charr, with most tags lost during the first 10 days. Small rockpool fishes, *Girella elevata* and *Bathygobius cocosensis,* experienced very low retention of 32±20% after 90 days under laboratory conditions (Griffiths 2002). In my study, size-dependent tag loss could not be assessed because only one tag was shed in both lab and field environments.

Tag visibility was excellent throughout both the tank and mark-recapture studies. The main problem with reading VIalpha tags is that tissue pigmentation can sometimes obscure the visibility of the code. Olsen et al. (2004) found that approximately 33% of tags were partly hidden behind pigmented tissue of hatchery juvenile cod though the codes were readable with the use of a blue light and amber glasses. Similar visual aids were sometimes required to view tags on marked rockpool fishes after 90 days (Griffiths 2002). Isley et al. (2004) found visibility was improved using slightly larger VIalpha tags and less than 0.1% were unreadable due to pigmentation. In my study, all tags were readable in the lab and in the field.

Mortality associated with the VIalpha tagging technique was low for age-0 Greenland cod with 82% survival after 18 days under lab conditions. Fish species tagged with soft VIalpha tags typically have high survival rates. High survival has been observed in juvenile Atlantic cod (96% survival over 150 days, Olsen et al. 2004), rainbow trout (93%; Isely et al. 2004), Arctic charr (96-98%; Rikardsen et al. 2002), and intertidal fishes (80±5%; Griffiths 2002). Observed mortalities during my study were attributed to handling, tank conditions, and(or) aggressive behaviour of confined fish.

In summary, the mortality rate of age-0 Greenland cod ($M = 0.021\ day^{-1}$) inhabiting Newman Sound was higher than those reported for older conspecifics and Atlantic cod juveniles. High mortality rates may be attributed to high predation, uncertainties in onshore-offshore movements, or uncertainties in long-term handling and containment stress. As with older conspecifics, juvenile Greenland cod exhibited low movement rates, remaining near the point of release, though some evidence of diel migrations was observed. VIalpha tagging is an appropriate method for mark-recapture studies of juvenile Greenland cod as small as 80 mmSL and provides high tag retention, visibility, and survival for marked individuals. There seems to be a negative effect on growth; however, decreased growth rates of tagged cod may be attributed to handling and containment stress.

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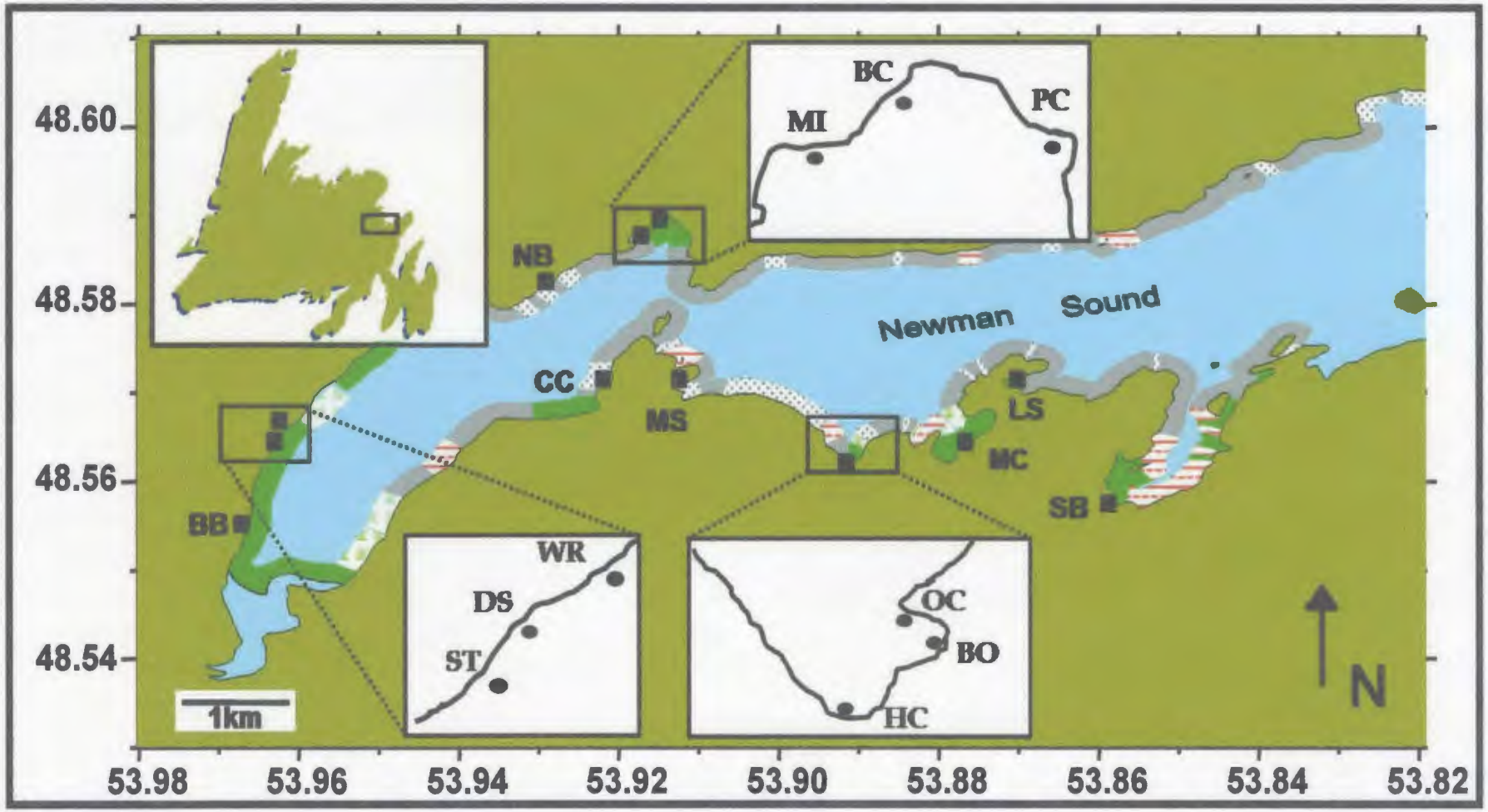

Figure 3.1: Map of the study area, Newman Sound, Bonavista Bay, Newfoundland. The three marking areas - Dockside (DS), Buckley's Cove (BC), and Boulder Beach (BO) - are enlarged with the marking and adjacent monitoring sites depicted as circles. Also featured are the 12 bi-weekly seining sites, represented as squares. Eight bi-weekly sites [Big Brook (BB), DS, Whiterock (WR), Mistaken Cove (MI), BC, Hefferns Cove (HC), Minchins Cove (MC), and South Broad Cove (SB)] have eelgrass habitat, shown with light green colouration, while the remaining four [Cannings Cove (CC), Newbridge Cove (NB), Mount Stamford (MS), and Little South Broad Cove (LS)] have no appreciable eelgrass.

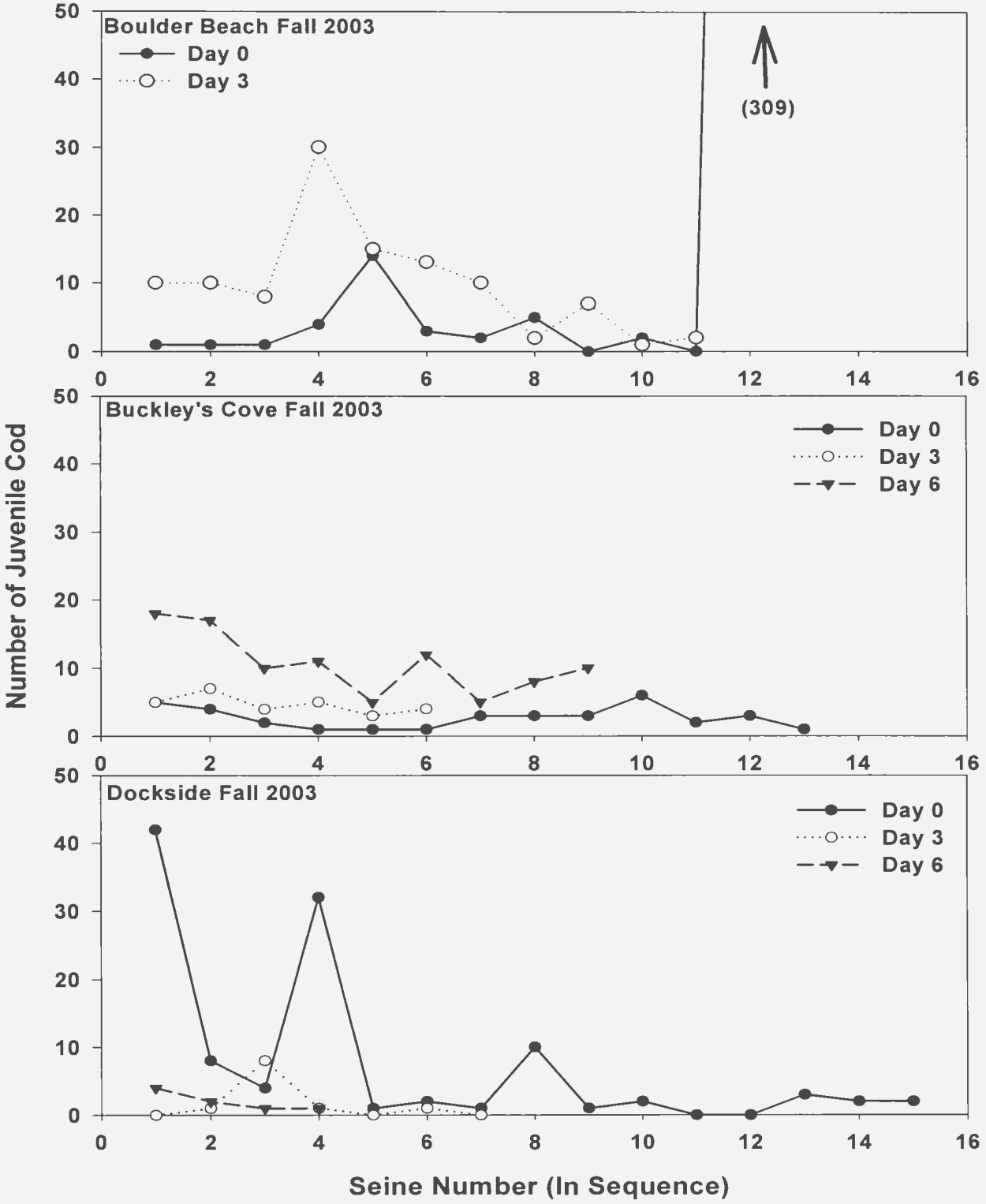

Figure 3.2: Number of juvenile Greenland cod collected via beach seine for tagging purposes at Boulder Beach, Buckley's Cove, and Dockside over several days in Fall 2003.

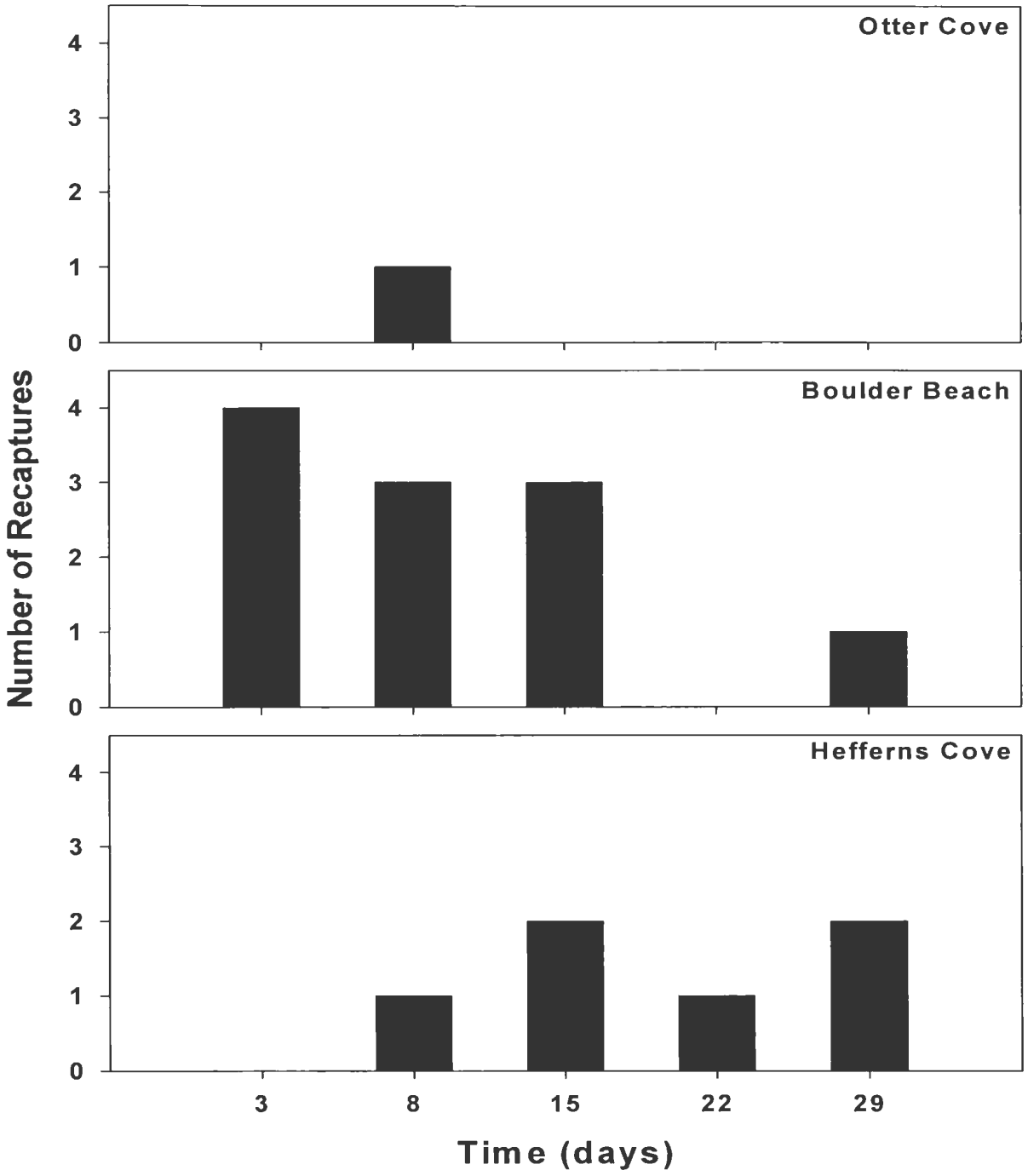

Figure 3.3: The dispersion over time of age-0 Greenland cod tagged at Boulder Beach during Fall 2003. The middle graph represents the tagging site (Boulder Beach) and the upper and lower graphs depict the recaptures collected at the adjacent monitoring sites (Otter Cove and Heffern's Cove, respectively).

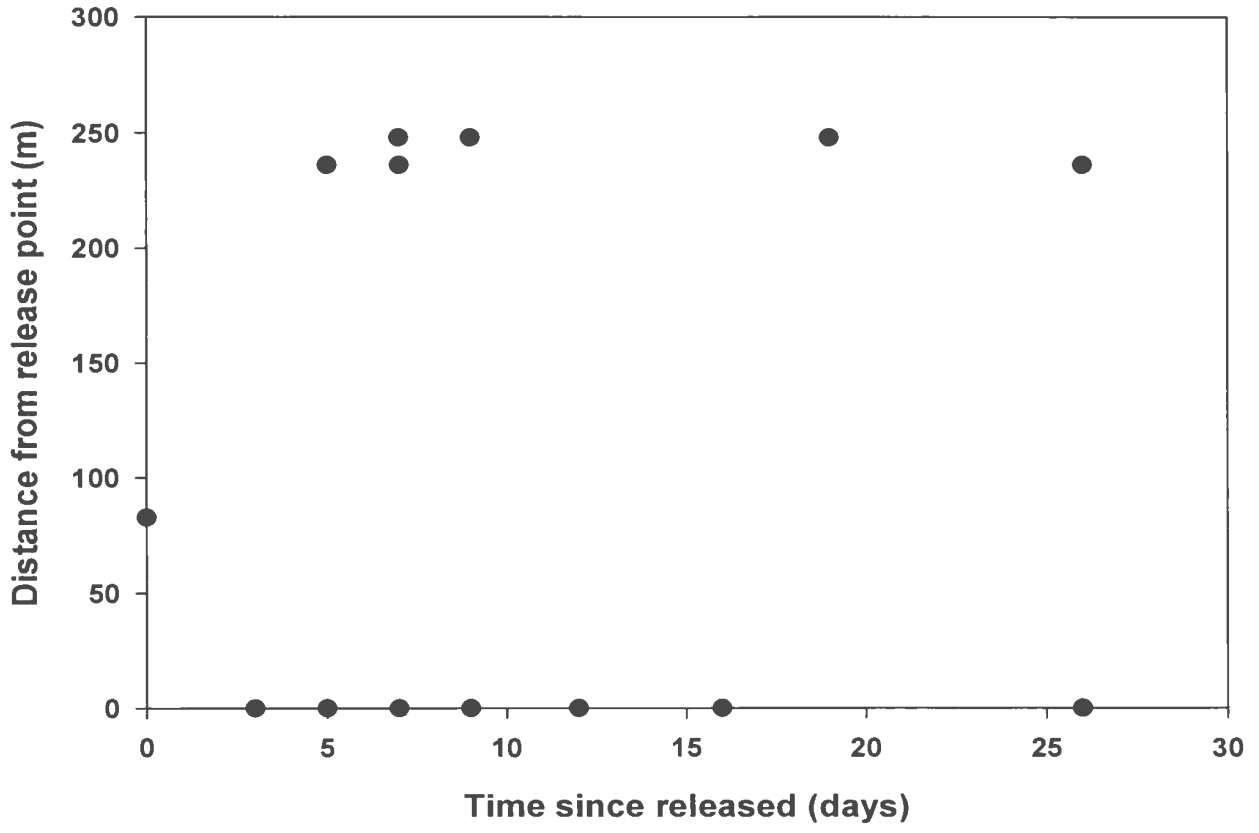

Figure 3.4: The distance travelled (m) by VIalpha tagged age-0 Greenland cod, plotted against time since release (days).

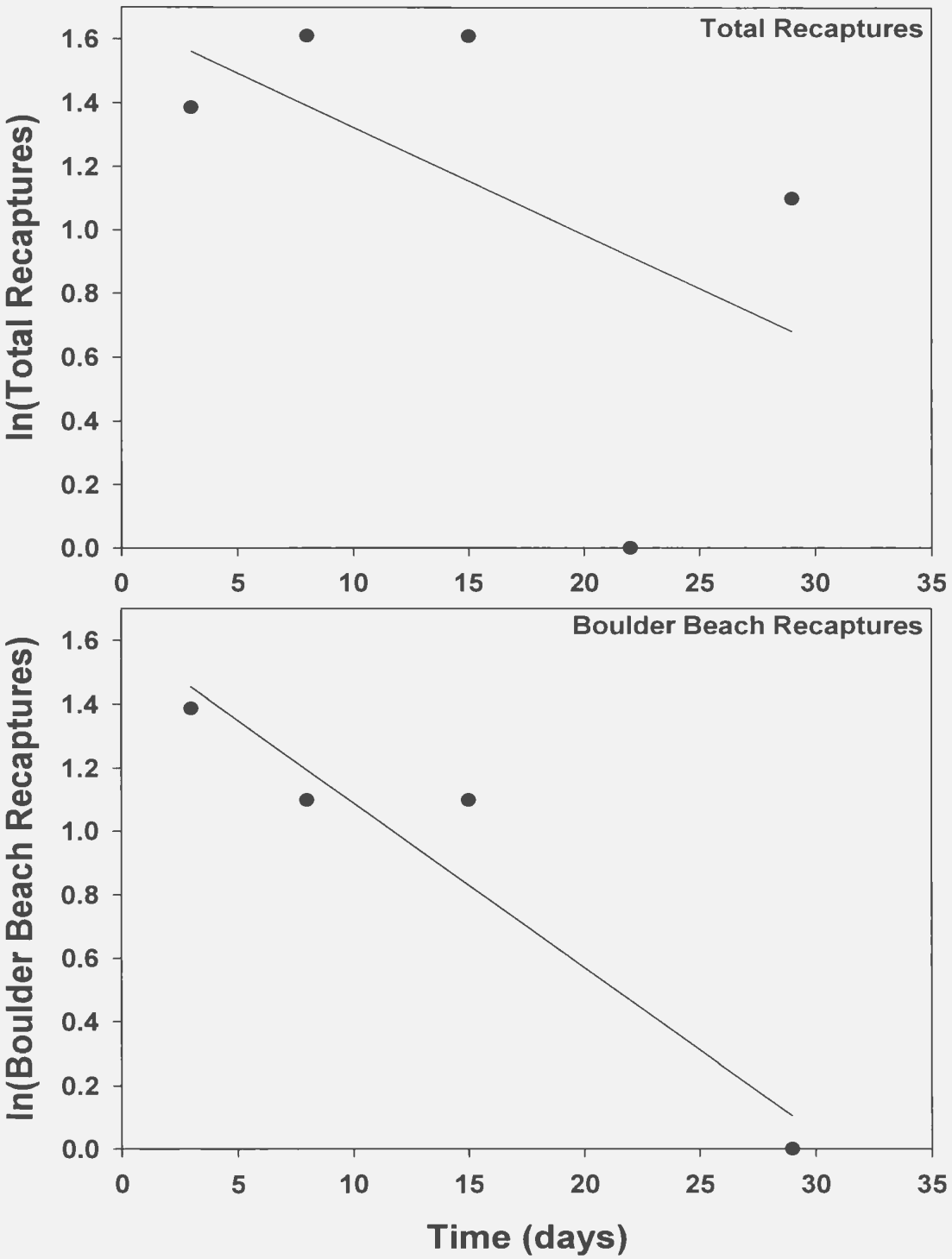

Figure 3.5: Catch curve analysis of recaptured VIalpha tagged cod. The slopes of the regression lines are estimates of apparent total mortality (Z; day^{-1}) when constant mortality rates are assumed (Total recaptures: $Z = 0.034\ day^{-1}$, $r^2 = 0.278$; Boulder Beach recaptures: $Z = 0.054\ day^{-1}$, $r^2 = 0.915$).

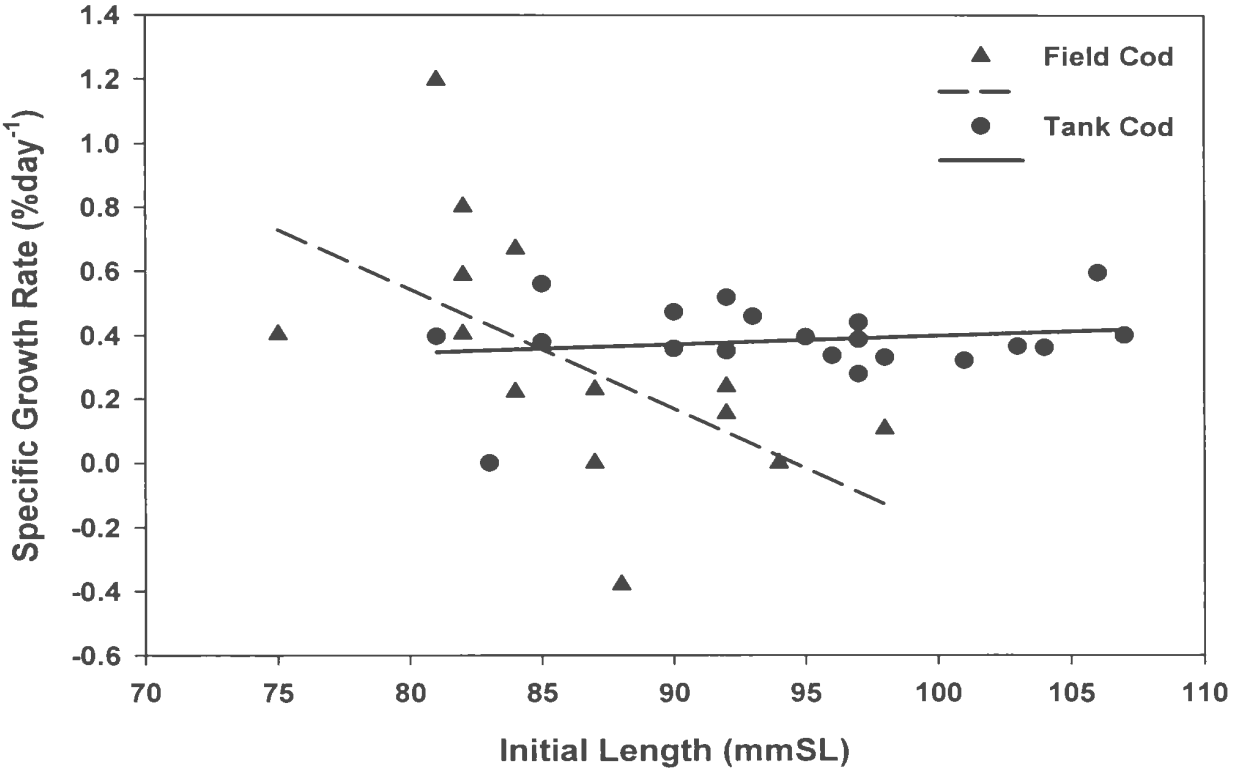

Figure 3.6: The effect of initial length (mmSL) on specific growth rates (%day^{-1}) for tank VIalpha tagged age-0 Greenland cod (circles) and recaptured VIalpha tagged age-0 Greenland cod (triangles). An analysis of covariance indicated that the relationship between SGR and initial tagging length was significantly different when field cod (dashed line) were compared to tank cod (solid line).

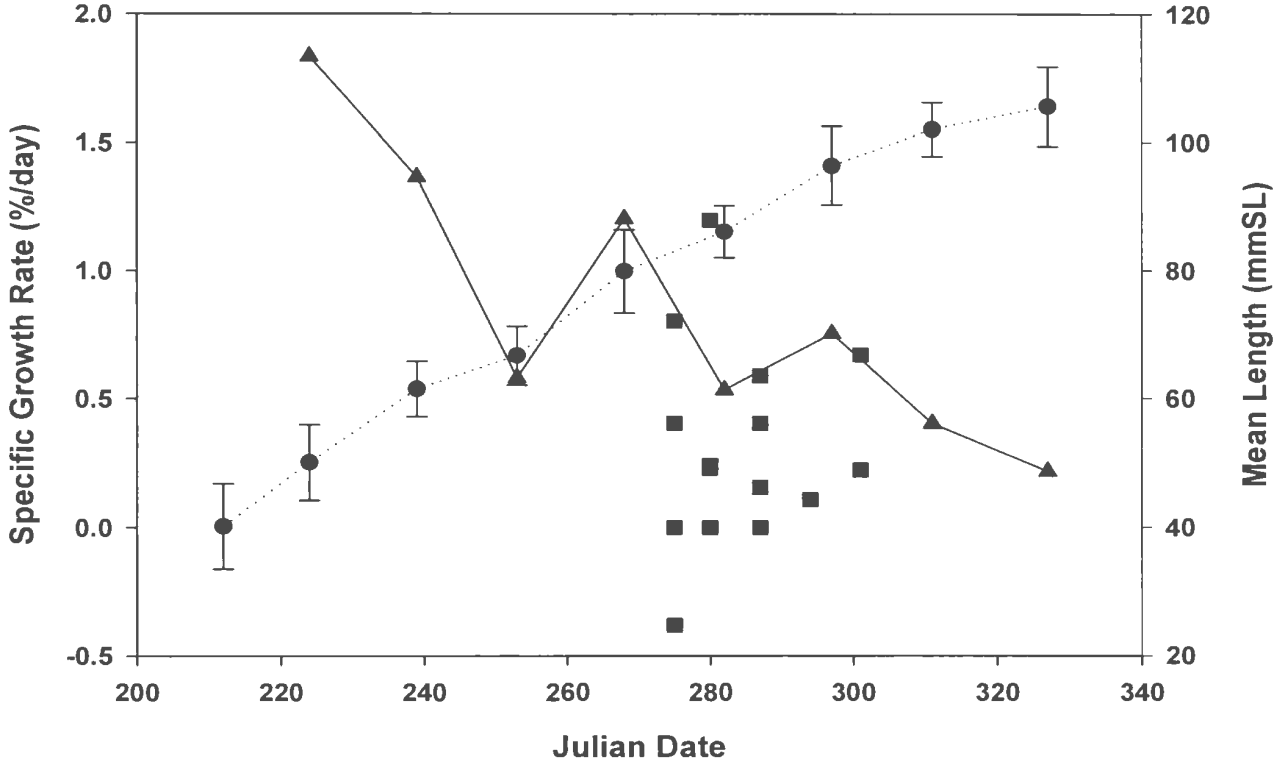

Figure 3.7: The change in specific growth rate (%day^{-1}) of untagged and tagged juvenile cod. Specific growth rates for untagged wild cod (triangles) were determined from mean lengths of age-0 Greenland cod collected during bi-weekly sampling at Heffern's Cove. Tagged cod (squares) are depicted as individual specific growth rates. Mean lengths (mmSL) with standard deviations for cod collected during bi-weekly sampling are included (circles).

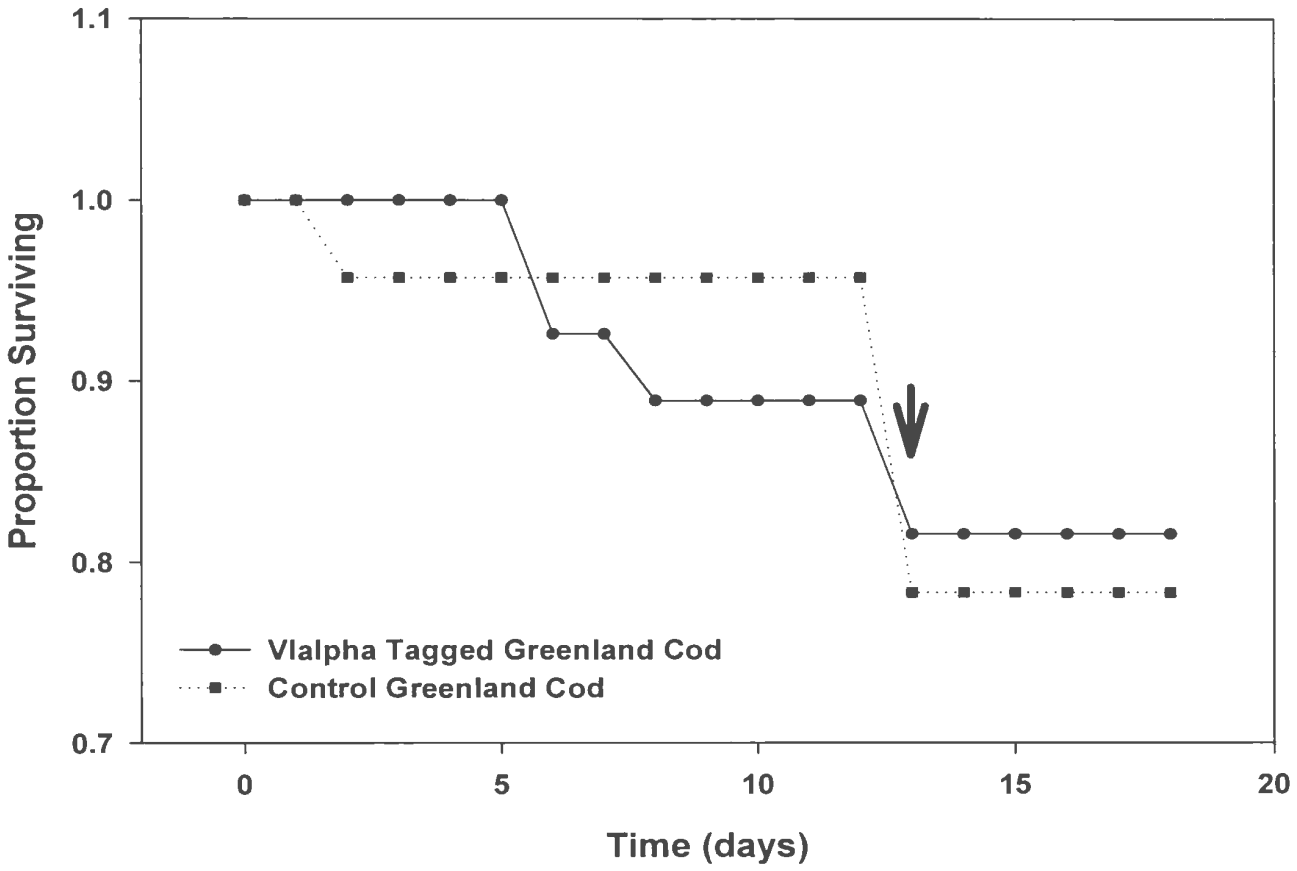

Figure 3.8: Survival of VI alpha tagged age-0 Greenland cod (n=27) and untagged controls (n=23) over the duration of the tank study conducted at the Marine Interpretation Centre, Terra Nova National Park, Newfoundland. Arrow indicates when cod exhibiting severe caudal injuries ("fin rot") were removed and killed.

Table 3.1: Summary data of recaptured VIalpha tagged age-0 Greenland cod. Tag codes in bold italics indicate multiple recaptures. Recapture sites in bold represent cod recaptured at adjacent monitoring sites. One cod (#17), identified by a caudal fin clip, shed its tag and was speculated as being marked at Boulder Beach based on low movements observed for juvenile cod.

Recapture #	Tag Code	Tagging Date (mm/dd/yy)	Tagging Site	Recapture Date (mm/dd/yy)	Recapture Site
1	S36	09/29/2003	Boulder Beach	10/02/2003	Boulder Beach
2	S37	09/29/2003	Boulder Beach	10/02/2003	Boulder Beach
3	S02	09/29/2003	Boulder Beach	10/02/2003	Boulder Beach
4	R28	09/29/2003	Boulder Beach	10/02/2003	Boulder Beach
5	H04	10/02/2003	Boulder Beach	10/07/2003	**Hefferns Cove**
6	R11	09/29/2003	Boulder Beach	10/07/2003	Boulder Beach
7	S32	09/29/2003	Boulder Beach	10/07/2003	Boulder Beach
8	H59	10/02/2003	Boulder Beach	10/07/2003	Boulder Beach
9	***R11***	09/29/2003	Boulder Beach	10/07/2003	**Otter Cove**
10	S34	09/29/2003	Boulder Beach	10/14/2003	**Hefferns Cove**
11	***S32***	09/29/2003	Boulder Beach	10/14/2003	**Hefferns Cove**
12	S05	09/29/2003	Boulder Beach	10/14/2003	Boulder Beach

Table 3.1 (continued): Summary data of recaptured VIalpha tagged age-0 Greenland cod. Tag codes in bold italics indicate multiple recaptures. Recapture sites in bold represent cod recaptured at adjacent monitoring sites. One cod (#17), identified by a caudal fin clip, shed its tag and was speculated as being marked at Boulder Beach based on low movements observed for juvenile cod.

Recapture #	Tag Code	Tagging Date (mm/dd/yy)	Tagging Site	Recapture Date (mm/dd/yy)	Recapture Site
13	***S37***	09/29/2003	Boulder Beach	10/14/2003	Boulder Beach
14	S87	10/02/2003	Boulder Beach	10/14/2003	Boulder Beach
15	W68	10/02/2003	Boulder Beach	10/21/2003	**Hefferns Cove**
16	H07	10/02/2003	Boulder Beach	10/28/2003	**Hefferns Cove**
17	unknown	unknown	Boulder Beach??	10/28/2003	**Hefferns Cove**
18	S63	10/02/2003	Boulder Beach	10/28/2003	Boulder Beach
19	K84	10/08/2003	Buckley's Cove	10/15/2003	Buckley's Cove
20	K87	10/08/2003	Buckley's Cove	10/15/2003	Buckley's Cove
21	F23	10/01/2003	Dockside	10/04/2003	Dockside
22	L36	10/01/2003	Dockside	10/09/2003	**Stairs Beach**
23	***L36***	10/01/2003	Dockside	10/16/2003	**Stairs Beach**

Table 3.2: Initial length (mmSL), recaptured length, change in change, and time at large of age-0 Greenland cod recaptured at Boulder Beach. Specific growth rates (SGR) are presented as % day^{-1}. Codes in bold italics are multiple recaptures. R11 was recaptured twice in one day hence time at large was less than one day. *In situ* measurement error estimated as ±0.0027 mmSL.

Tag Code	Length at Capture	Length at Recapture	ΔLength	Time at Large	SGR (%day^{-1})
S36	88	87	-1	3	-0.381
S37	82	83	1	3	0.404
S02	87	87	0	3	0
R28	82	84	2	3	0.803
H04	87	88	1	5	0.229
R11	92	94	2	9	0.239
S32	94	94	0	9	0
H59	81	86	5	5	1.198
R11	94	94	0	<1	0
S34	92	93	1	7	0.154
S32	94	94	0	7	0
S05	75	80	5	16	0.403
S37	83	88	5	12	0.588
S87	87	87	0	12	0
W68	98	100	2	19	0.106
H07	84	100	14	26	0.671
S63	84	89	7	26	0.222
Mean	**87.3**	**89.9**	**2.6**	**9.8**	**0.273**

Table 3.3: Mean lengths (mmSL) of VIalpha tagged and control age-0 Greenland cod reared in controlled conditions.

	Tagged Greenland Cod			Control Greenland Cod		
Day	**n**	**Mean Length (mmSL)**	**Standard Deviation**	**n**	**Mean Length (mmSL)**	**Standard Deviation**
0	27	94.2	7.8	23	96.2	6.3
2	27	94.2	7.8	22	97.0	5.1
6	25	95.1	7.3	22	97.0	5.1
13	22	96.9	8.4	18	100.2	4.3
18	22	101.4	8.8	18	102.0	8.0

Chapter 4: Summary

4.1 Juvenile cod mortality and movement in Newman Sound

Age 0-1 cod experience high mortality rates, even in areas with protective vertical structure in Newman Sound. A natural mortality rate of 0.068 day^{-1} was estimated for age-1 Atlantic cod, suggesting that the population size of the cohort was reduced by nearly half on a weekly basis. Age-0 Greenland cod were observed to exhibit a natural mortality rate of 0.021 day^{-1}, nearly three times lower than the rate estimated for the older Atlantic cod. Juvenile cod preferentially settle in complex habitats (e.g., eelgrass, Laurel et al. 2003) where vertical structure can provide: (1) refuge from predators (Gotceitas et al. 1995, 1997; Hindell et al. 2000; Linehan et al. 2001; Laurel et al. 2003), (2) elevated food levels (Connolly 1994; Renkawitz 2005), (3) reduced physical exposure (Bell and Pollard 1989), and (4) increased water quality (Orth et al. 1984). Despite these benefits, juvenile cod nonetheless experience high mortality rates in eelgrass habitat, suggesting that mortality rates in other available habitats (i.e., mud, sand) are even worse. Available data on predation risk suggests this is indeed the case (Tupper and Boutilier 1995; Linehan et al. 2001; Laurel et al. 2003).

In many teleost populations, natural mortality is stage- and size-dependent, with younger age-classes experiencing higher rates than older, larger stages (Peterson and Wroblewski 1984). As fish age and grow, the susceptibility to density-independent mortality decreases, resulting decreased predation risk, increased resistence to starvation, and increased tolerance to environmental fluctuations (see review by Sogard 1997). During my study, age-1 Atlantic cod were typically smaller and more variable in size compared to

age-0 Greenland cod, which may explain the discrepancy between the mortality estimates for the two age-classes. Furthermore, size-dependent mortality related to handling stress may have elevated the estimate for age-1 Atlantic cod because individuals <80 mmSL were more vulnerable to this mortality than larger individuals. The mean lengths for age-1 Atlantic cod fin-clipped on Day 0 and Day 6 at Dockside during Spring 2003 were <80 mmSL, which suggests a large portion of these releases were prone to stressed-related mortality. Conversely, the mean lengths of VIalpha-tagged age-0 Greenland cod were larger than 80 mmSL, suggesting that these individuals were predominately tolerant to handling mortality.

Despite adjustments for handling mortality and emigration, the natural mortality rate determined for age-1 Atlantic cod in nearshore Newfoundland waters was high compared to published rates. The rate estimated for age-0 Greenland cod may also be overestimated, but cannot be verified because published rates are largely absent. Several uncertainties may have contributed to the overestimation of natural mortality rates during my study. For example, I estimated acute stressed-related mortality for juvenile cod over a period of a few days; however, delayed stressed-related mortality may be occurring weeks or months after release (Ricker 1949). Abnormal behaviour may be exhibited following a stressful event (Mesa and Schreck 1989), possibly leading to increased susceptibility to predation, reduced feeding efficiency, and decreased resistance to disease and environmental fluctuations, resulting in mortality rates being positively biased. Further study is required to quantify mortality directly or indirectly related to long-term handling stress for cod age 0-1 years. In addition, tagging mortality was negligible in tank studies;

however, indirect tagging-related mortality may have occurred for fin-clipped age-1 Atlantic cod and VIalpha-tagged age-0 Greenland cod released into the natural environment. It is unlikely the minute marks were visually observable to potential predators; but both techniques involve the infliction of wounds that may increase the probability of detection by potential predators using chemosensory cues. Similar scenarios have been proposed for cod during field studies that involve sonic tag implantation (Cote et al. 2001) and tethering (Linehan et al. 2001). A better assessment of tagging-related mortality would require the inclusion of known predators in tank studies to compare encounter rates of marked and unmarked individuals. In addition, uncertainties in temporary emigration may result in erroneous mortality estimates. Animals suspected to be dead or permanently emigrated may be moving in and out of the study area, leading to mortality values being overestimated. Age-1+ Atlantic cod undertake diel migrations from deep, cool waters inhabited during the day to shallow, warmer waters at night (Keats 1990; Cote et al. 2001). Higher captures of Greenland cod >100 mm occur at night than during the day in the shallow waters of James Bay (Morin et al. 1991), and similar movements are conducted by Greenland cod <100 mm in Newman Sound (personal observation). These "onshore-offshore" movements suggest temporary emigration occurred for both species during my study and possibly caused mortality rates to be positively biased. Sampling at night and in deeper water is recommended to determine the extent of diel migrations for age 0-1 cod in the Newfoundland coastal zone.

Juvenile cod, aged 0-1 years, exhibited small scale movements in nearshore habitat during my study - rarely moving more than a few hundred metres - regardless of age,

species, or season. These observations are consistent with the findings of other Northern Atlantic Ocean studies (Hjort 1914; Svasand and Krisitiansen 1990; Pihl and Ulmestrand 1993; Smedstad et al. 1994; Tupper and Boutilier 1995; Gotceitas et al. 1996; Gregory et al. 1997; Grant and Brown 1998; Skreslet et al. 1999). During the study period, marked cod were not recaptured outside of the coves where they were initially marked and released, which suggests that the probability of large-scale alongshore movements is low for age 0-1 cod during late spring (June-July) and early fall (October-November). The limited nearshore movements of age-0 Greenland cod and age-1 Atlantic cod are consistent with the life history movement patterns of each respective species. Larger Greenland cod juveniles (age 1-2) and adults (age 3+) have been described as non-migratory, non-schooling, sedentary fish (Mikhail and Welch 1989; Morin et al. 1991; Nielsen and Andersen 2001) that remain in home inlets for life (Mikhail and Welch 1989). Demersal eggs are spawned beneath the ice in the vicinity of nearshore nursery habitats (Mikhail and Welch 1989; Methven et al. 2001), which are subsequently occupied by benthic age-0 juveniles (Ings 2005). Over their life history, Greenland cod appear limited to relatively small scale movements compared to Atlantic cod. The scale of movement varies over the life history of Atlantic cod. Spawning occurs tens to hundreds of kilometres offshore in deep waters and the pelagic eggs and larvae are transported to nearshore nursery habitats by winds and currents. Settlement occurs in the nearshore during multiple recruitment pulses (Methven and Bajdik 1994; Grant and Brown 1998; Gregory et al. 2002) and small scale movements are exhibited by benthic juveniles, aged 0-1, associated with structurally complex habitats (e.g., eelgrass, macroalgae). As body size increases with age, the affinity

for structural habitats decrease and the size of home ranges increase as seasonal and spawning migrations occur (Cote et al. 2001).

The limited small-scale movements of juvenile cod may result from density-dependent habitat selection. Laurel et al. (2004) suggested that the probability of large-scale movements (> 1000 m) was high for young cod in Newman Sound during years with high cod densities. These authors speculated that saturation of optimal nearshore habitats by conspecifics forced juvenile cod to: (1) occupy suboptimal habitats with limited availability of vertical structure (e.g., mud, sand) and (2) form highly mobile shoaling aggregations to offset the elevated predation risk experienced in such suboptimal habitats. In 2002 and 2003 - the years of my study- juvenile cod abundances in Newman Sound were low compared with previous years (Gregory et al. 2003, 2005), which may explain why I did not observe any evidence of large-scale alongshore movements for age-0 Greenland cod and age-1 Atlantic cod.

4.2 Implications and future study

The mortality rates I estimated in this study will provide fisheries managers and marine ecologists with quantified values of juvenile cod survival in coastal Newfoundland waters. Furthermore, the development of an age-dependent mortality model will allow investigators to predict mortality rates for juveniles, particularly individuals aged 0-3 years. However, further study is warranted to determine whether the mortality rates observed for juvenile cod in Newman Sound are similar to those experienced by young cod in other coastal areas of Newfoundland. The mortality rates observed in my study occurred over small spatial (<1000 m^2) and temporal (i.e., days to weeks) scales. Conclusions based on

small scale studies are not necessarily transferable to larger scale processes or vice versa (Thrush et al. 1997; Schneider 2001).

The distribution of juvenile cod habitat, such as eelgrass, is non-uniform and may vary with geographic location, environmental conditions (e.g., temperature, salinity), bottom geology and morphology, wind-generated wave dynamics, tidal currents, water depth, light penetration, and storm severity (Kelly 1980; Turner et al. 1999). These factors induce eelgrass habitats to range in complexity from large continuous meadows (i.e., low 2-D complexity) to small sparse patches (i.e., high 2-D complexity). Juvenile cod abundance is related to the 2-D complexity of eelgrass habitat (Wells 2002; Hammond 2003). The relationship between juvenile cod abundance and habitat complexity depends on whether fish can hide from patrolling predators while accessing benthic prey items (Wells 2002). For example, low complexity habitats (i.e., dense eelgrass meadows) provide sufficient shelter, but restrict access to benthic prey, whereas highly complex habitats (i.e., sparse eelgrass patches) offer unrestricted access to prey but limited protection. Juvenile cod abundance is highest in habitats of intermediate complexity where the ability to hide and forage appear balanced (Wells 2002; Hammond 2003). In my study, mortality rates were estimated for cod at eelgrass sites of intermediate complexity according to the criteria of Wells (2002). The high abundances of juvenile cod in eelgrass with intermediate complexity, despite high mortality rates, suggest that survival may be greatly reduced in eelgrass with low or high complexities. Further work is required to determine whether juvenile cod mortality is influenced by habitat complexity.

The low movement rates of juvenile cod in nearshore habitats suggest that Marine

Protected Areas (MPAs) will be an effective conservation measure for cod. In Newfoundland, MPAs have been proposed near Gilbert Bay, Eastport, and Leading Tickles (Morris and Power 2004). Juvenile cod habitat, in the form of vegetation, has been documented at all three localities (C. Morris, Department of Fisheries and Oceans, personal communication). The distribution of young cod in shallow waters during spring and fall, along with low movement, will increase the juvenile cod survivorship. However, protection may decrease when age-0 Greenland cod and age-1 Atlantic cod presumably move to deeper waters in late fall and early summer, respectively. Further study is needed to determine the mortality rates of juvenile cod when distributions shift to deeper waters where protective structure (i.e., macroalgae, cobble) may be unavailable. My study has shown that age 0-1 cod exhibit high site fidelity within eelgrass habitats where they exhibit higher mortality than expected from published accounts, which suggests that predation mortality in other habitats is worse.

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Appendix 1

Table A1: The number of seines used to recapture fin-clipped age-0 Greenland cod (*Gadus ogac*) for each sampling day at Buckley's Cove, Mistaken Cove, and Pipers Cove during the period of October 3-20, 2002. Day 0 refers to the day juvenile cod were collected for marking purposes.

Site	Number of Seines						
	October 3 (Day 0)	October 4 (Day 1)	October 6 (Day 3)	October 8 (Day 5)	October 10 (Day 7)	October 16 (Day 13)	October 20 (Day 17)
Buckley's Cove	4	7	5	1	1	1	1
Mistaken Cove	0	1	1	1	1	1	1
Pipers Cove	0	1	1	1	1	1	1

Table A2: The number of seines used to recapture fin-clipped age-1 Atlantic cod (*Gadus morhua*) for each sampling day at Dockside, Stairs Beach, and Whiterock during the period of June 7 to July 17, 2003. Day 0 refers to the day juvenile cod were collected for marking purposes.

Site	Number of Seines						
	June 7 (Day 0)	June 10 (Day 3)	June 13 (Day 6)	June 21 (Day 14)	July 3 (Day 26)	July 10 (Day 32)	July 17 (Day 40)
Dockside	9	9	3	4	3	3	3
Stairs Beach	0	4	1	4	3	2	3
Whiterock	0	2	2	5	3	1	2

Table A3: The number of seines used to recapture fin-clipped age-1 Atlantic cod (*Gadus morhua*) for each sampling day at Buckley's Cove, Mistaken Cove, and Pipers Cove during the period of June 6 to July 17, 2003. Day 0 refers to the day juvenile cod were collected for marking purposes.

Site	Number of Seines							
	June 6 (Day 0)	June 9 (Day 3)	June 12 (Day 6)	June 19 (Day 13)	June 26 (Day 20)	July 4 (Day 28)	July 8 (Day 33)	July 17 (Day 41)
Buckley's Cove	10	15	4	5	2	3	2	3
Mistaken Cove	0	3	1	5	3	2	2	3
Pipers Cove	0	4	2	3	2	2	3	3

Appendix 2

Jolly-Seber Notation and Formulae

If the assumptions of the Jolly-Seber method are justified, the proportion of marked or tagged specimens in the captured sample should equal that in the actual population, N_i:

$$\frac{m_i}{n_i} \cong \frac{M_i}{N_i} \qquad \text{(A1.1)}$$

where m_i is the number of marked animals captured in the ith sample, n_i represents the total number of animals captured in the ith sample, and M_i in the number of marked animals in the population when the ith sample is collected. M_i is estimated as $\hat{M}_i$, which is computed from with the number of animals released after the ith sample (R_i), the number of animals released at i that are recaptured (r_i), the number of animals captured before i, *not* captured at i, and captured again after i (z_i), and m_i:

$$\hat{M}_i = \frac{R_i z_i}{r_i} + m_i \qquad \text{(A1.2)}$$

After the marked population sizes $\hat{M}_i$, are estimated, manipulation of the previous equation yields an estimator for the population size:

$$\hat{N}_i = \frac{n_i \hat{M}_i}{m_i} \qquad \text{(A1.3)}$$

Population sizes are not directly required for estimation of ϕ_i, the probability of survival from sample i to sample $i+1$. Instead, the survival rate is estimated by comparing the number of marked individuals present in the population immediately after sample i

with the marked population before sample i, after correcting for removals or accidental deaths occurring during sample i:

$$\hat{\phi}_i = \frac{\hat{M}_{i+1}}{\hat{M}_i + R_i - m_i} \qquad \text{(A1.4)}$$

The Jolly-Seber survival rate estimator actually provides an apparent survival rate as it does not distinguish between animals dying and animals simply leaving the study area. For model simplicity, animals leaving the study area are assumed permanent losses to the system. If migration patterns can be evaluated, the apparent survival rate can be adjusted to provide an estimate of true survival. Aside from estimating losses to the study area, the JS method can also assess recruitment, B_i, between sample i and sample $i+1$:

$$\hat{B}_i = \hat{N}_{i+1} - \hat{\phi}_i(\hat{N}_i - n_i + R_i) \qquad \text{(A1.5)}$$

The precision of estimates depend on whether the animals being studied can be efficiently collected in the area of habitation by the sampling gear. The probability of capture, $\hat{p}_i$, can be estimated from the proportion of marked (m_i), or total (n_i), animals alive at sample i that are captured in i:

$$\hat{p}_i = \frac{m_i}{\hat{M}_i} = \frac{n_i}{\hat{N}_i} \qquad \text{(A1.6)}$$

Probability of capture should not be confused with the recapture proportion (RP_i), routinely calculated as $RP_i = m_i/n_i$, though both parameters are useful as sampling intensity indicators (Fitz and Wiegert 1992).

The ϕ_i and $\hat{p}_i$ are maximum likelihood estimators and all estimates described above can appear reasonable despite being biased. For this reason, approximately

unbiased estimators have been devised by Seber (1982) for $\widetilde{\phi}_i, \widetilde{N}_i, \widetilde{B}_i$, and $\widetilde{M}_i$:

$$\widetilde{\phi}_i = \frac{\widetilde{M}_{i+1}}{\hat{M}_i + R_i - m_i} \tag{A1.7}$$

$$\widetilde{N}_i = \frac{(n_i + 1)\widetilde{M}_i}{m_i + 1} \tag{A1.8}$$

$$\widetilde{B}_i = \widetilde{N}_{i+1} - \widetilde{\phi}_i(\widetilde{N}_i - n_i + R_i) \tag{A1.9}$$

$$\widetilde{M}_i = \frac{(R_i + 1)z_i}{r_i + 1} + m_i \tag{A1.10}$$

Jolly (1982) reported the following unbiased estimator for p_i:

$$\widetilde{p}_i = \frac{m_i}{\widetilde{M}_i} \tag{A1.11}$$

Approximate asymptotic variances and covariances for Jolly-Seber formulae are calculated by the program JOLLY. Pollock et al., (1990) stated that the variances include estimation variability, or the variation resulting from capture probabilities not equalling 1. They used the symbol $\text{var}\left(\hat{\theta}_i|\theta_i\right)$ to distinguish from Seber's (1982) $\text{var}(\hat{\theta}_i)$ that incorporated sampling and nonsampling variation associated with birth and death. The expected or mean value of a particular parameter is denoted by E(*). Variance equations are shown below and all covariance terms, excluding ϕ_i and B_i, are zero:

$$\text{var}\left(\hat{M}_i|M_i\right) = \left[M_i - E(m_i)\right]\left[M_i - E(m_i) + R_i\right]\left[\frac{1}{E(r_i)} - \frac{1}{R_i}\right] \tag{A1.12}$$

$$\operatorname{cov}\left(\hat{\phi}_i \middle| \hat{\phi}_{i+1}\right) = -\phi(\phi_{i-1}) \frac{\left[M_{i+1} - E(m_{i-1})\right]}{M_{i+1}} \left[\frac{1}{E(r_{i+1})} - \frac{1}{R_{i+1}}\right] \tag{A1.13}$$

$$\operatorname{var}\left(\hat{N}_i \middle| N_i\right) = N_i\left[N_i - E(n_i)\right]\left\{\frac{M_i - E(m_i) + R_i}{M_i}\left[\frac{1}{E(r_i)} - \frac{1}{R_i}\right] + \frac{(N_i - M_i)}{N_i E(m_i)}\right\} \tag{A1.14}$$

$$\operatorname{var}\left(\phi_i \middle| \phi_i\right) = \phi^2\left\{\begin{array}{l}\dfrac{\left[M_{i+1} - E(m_{i+1})\right]\left[M_{i+1} - E(m_{i+1}) + R_{i+1}\right]}{(M_{i+1})^2}\left[\dfrac{1}{E(r_{i+1})} - \dfrac{1}{R_{i+1}}\right] \\ + \dfrac{\left[M_i - E(m_i)\right]}{\left[M_i - E(m_i) + R_i\right]}\left[\dfrac{1}{E(r_i)} - \dfrac{1}{R_i}\right]\end{array}\right\} \tag{A1.15}$$

$$\operatorname{var}\left(\hat{p}_i \middle| p_i\right) = p_i^2\left(1 - p_i\right)^2\left[\frac{1}{E(r_i)} - \frac{1}{R_i} + \frac{1}{E(m_i)} + \frac{1}{E(z_i)}\right] \tag{A1.16}$$

$$\operatorname{cov}\left(\hat{B}i, \hat{B}_{i+1}\right) = \left\{\begin{array}{l}-\phi_{i+1}\dfrac{\left[N_{i+1} - E(n_{i+1})\right](N_{i+1} - M_{i+1})}{N_{i+1}} \\ \cdot\left[\dfrac{B_i R_{i+1}}{M_{i+1}}\left(\dfrac{1}{E(r_{i+1})} - \dfrac{1}{R_{i+1}}\right) + \dfrac{N_{i+1}}{E(m_{i+1})}\right]\end{array}\right\} \tag{A1.17}$$

$$\left(\operatorname{var}\hat{B}_i \middle| \hat{B}_i\right) = \left\{\begin{array}{l}B_i^2\left[M_{i-1} - E(m_{i-1})\right]\dfrac{\left[M_{i-1} - E(m_{i-1}) + R_{i-1}\right]}{(M_{i-1})^2} \\ \cdot\left[\dfrac{1}{E(_{i-1})} - \dfrac{1}{R_{i-1}}\right] + \dfrac{\left[M_i - E(m_i)\right]}{\left[M_i - E(m_i) + R_i\right]} \cdot \dfrac{\left[\phi R_i(N_i - M_i)\right]^2}{M_i^2} \\ \cdot\left[\dfrac{1}{E(r_i)} - \dfrac{1}{R_i}\right] + \dfrac{\left[N_i - E(n_i)\right](N_{i-1} - B_i)(N_i - M_i)\left(1 - \phi_i\right)}{N_i\left[M_i - E(m_i) + R_i\right]} \\ \cdot\left[\dfrac{N_{i+1}\left[N_{i+1} - E(n_{i+1})\right]\left[N_{i+1} - M_{i+1}\right]}{N_{i+1}E(m_{i+1})}\right] + \dfrac{\phi_i^2 N_i\left[N_i - E(n_i)\right](N_i - M_i)}{N_i E(m_i)}\end{array}\right\} \tag{A1.18}$$

Pollock et al., (1990) included a means to calculate the full variance of ϕ_i:

$$\text{var}(\hat{\phi}_i) = \text{var}\left(\hat{\phi}_i | \phi_i\right) + \frac{\phi_i(1-\phi_i)}{N_i - n_i + R_i} \qquad \text{(A1.19)}$$

because they felt that biologists are more interested in the ϕ_i itself, and that variance estimates including sampling and nonsampling variation would be of interest.

All formulae described thus far is applicable to the JS full model, also commonly referred to as Model A, whereby $\hat{\phi}_i$ and $\hat{p}_i$ vary with time. More restricted models have been devised by Jolly (1982) in an attempt to increase the precision of parameter estimators, and these differ from the full model by making $\hat{\phi}_i$ constant (Model B) or $\hat{p}_i$ constant (Model C) or both (Model D). The use of these models may increase precision; however, when applied, the restrictions must be biologically reasonable or the estimates will be biased. The program JOLLY provides an option to analyse mark-recapture using Models A, B, and D. Two other models, labelled as Model A' and Model 2, are available in JOLLY and are commonly known as the Death Only Model and the Temporary Trap Response Model, respectively. Models A' and 2 were not used in the analysis of juvenile cod mark-recapture data. A further advantage of the program JOLLY, other than being able to analyse mark-recapture data with different estimation models, is it conducts chi-square goodness-of-fit tests to determine the most appropriate, biologically reasonable model. These tests were developed and outlined by Brownie et al. (1986).

Appendix 3

Table A4: Method B table determined by program JOLLY for age 0 Greenland cod fin-clipped at Buckley's Cove in October 2002. R_i denotes the number of animals released after the *i*th sample; z_i denotes the number of animals captured before *i*, not captured at *i*, and captured again in some later sample.

Time of Last Capture	**Time of Recapture**			
	1	**2**	**3**	**4**
1	**0**	21	5	3
2		**0**	4	0
3			**0**	2
4				**0**
Marked (m_i)	0	21	9	5
Unmarked (u_i)	364	266	280	40
Total Caught (n_i)	364	287	289	45
Released (s_i)	331	287	289	45
R_i	29	4	2	0
z_i	0	8	3	0

Table A5: Method B table generated by program JOLLY for age 1 Atlantic cod fin-clipped at Dockside in June 2003.

Time of Last Capture		**Time of Recapture**		
	1	**2**	**3**	**4**
1	**0**	30	11	1
2		**0**	10	2
3			**0**	8
4				**0**
Marked (m_i)	0	30	21	11
Unmarked (u_i)	272	189	259	68
Total Caught (n_i)	272	219	280	79
Released (s_i)	271	209	280	79
R_i	42	12	8	0
z_i	0	12	3	0

Table A6: Method B table determined with program JOLLY for age 1 Atlantic cod fin-clipped at Buckley's Cove in June 2003.

Time of Last Capture	**Time of Recapture**			
	1	**2**	**3**	**4**
1	**0**	22	23	2
2		**0**	9	3
3			**0**	3
4				**0**
Marked (m_i)	0	22	32	8
Unmarked (u_i)	237	193	214	30
Total Caught (n_i)	237	215	246	38
Released (s_i)	236	206	238	38
$\mathbf{R_i}$	47	12	3	0
$\mathbf{z_i}$	0	25	5	0

Table A7: Method B table generated by program JOLLY for pooled mark-recapture data from age 1 Atlantic cod fin-clipped at Buckley's Cove and Dockside in June 2003.

Time of Last Capture	**Time of Recapture**			
	1	**2**	**3**	**4**
1	**0**	52	34	3
2		**0**	19	5
3			**0**	11
4				**0**
Marked (m_i)	0	52	53	19
Unmarked (u_i)	509	382	473	68
Total Caught (n_i)	509	434	526	87
Released (s_i)	507	415	518	87
R_i	89	24	11	0
z_i	0	37	8	0

Appendix 4: SAS output with ANCOVA table and residuals vs. fits plot for the juvenile cod age-dependent natural mortality model.

Model:
$\ln M = \beta_o + \beta_{Age} * \ln(Age)$

Symbols:
M = instantaneous natural mortality rate (day^{-1})
Age = age of juvenile cod in days

Results:
Distribution: Gamma
Link Function: Log
Dependent Variable: M
Observations Used: 17

Analysis Of Parameter Estimates

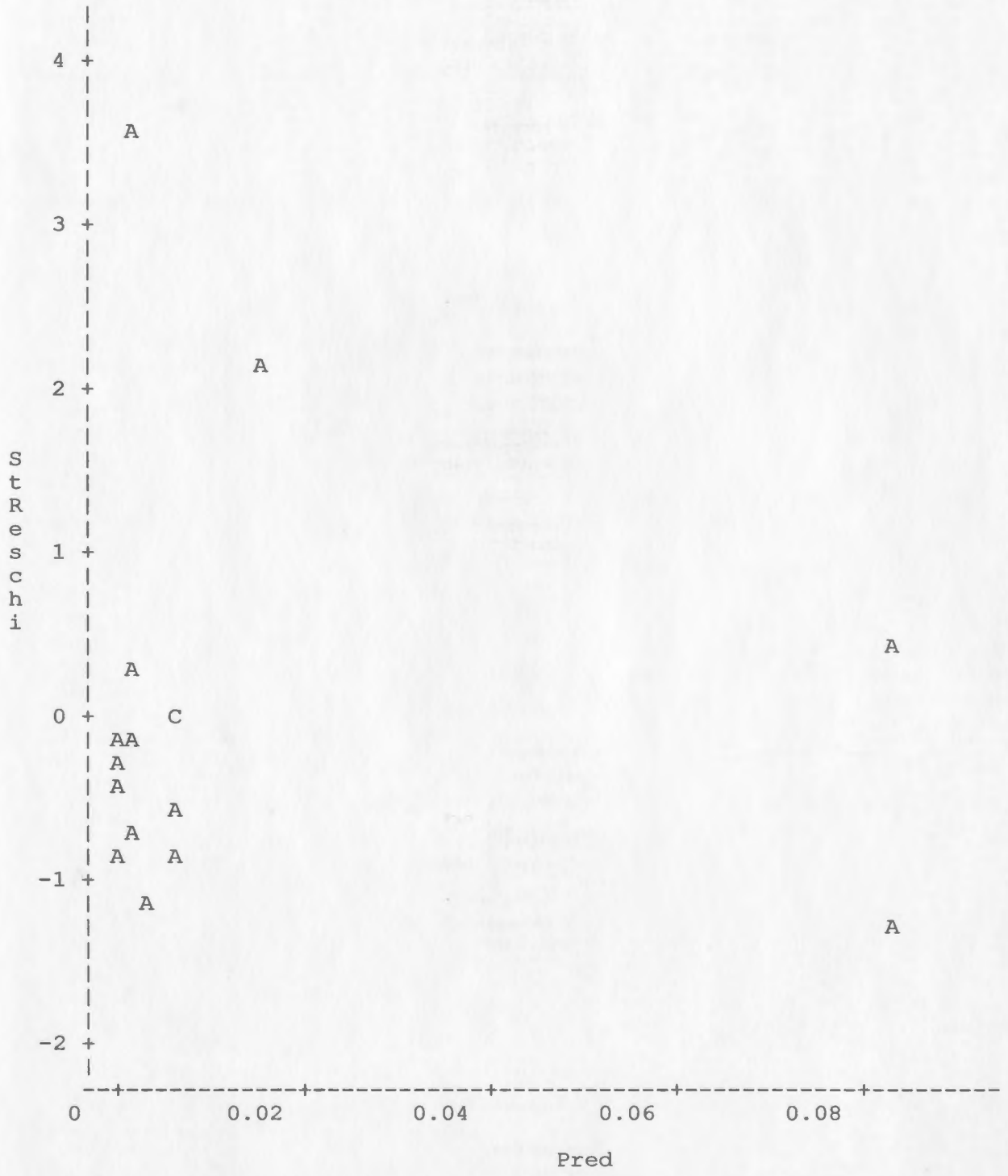
Parameter	DF	Estimate	Standard Error	Wald 95% Confidence Limits		χ^2
Intercept	1	10.3856	2.3361	5.8068	14.9644	19.76
age	1	-2.4724	0.3577	-3.1735	-1.7713	47.77
Scale	1	1.3808	0.4284	0.7517	2.5365	

LR Statistics For Type 3 Analysis

Source	DF	χ^2	Pr > χ^2
age	1	28.22	<.0001

Therefore the regression equation is:
$M = e^{-2.47Age + 10.39}$

Plot of Streschi*Pred. Legend: A = 1 obs, B = 2 obs, etc.



Appendix 5:

Table A8: Summary data for age-0 Greenland cod (*G. ogac*) VIalpha tagged at Newman Sound, Newfoundland, during Fall 2003. Numbers of cod marked, mean lengths, and standard deviations (SD) represent cod released during the tagging study. Percent recapture was calculated as the number of recaptures divided by the number of cod marked and multiplied by 100.

Date	Site	Event	Tag Codes Used	Number of Cod Marked	Mean Length (mmSL)	SD	Number of Recaptures	Percent Recapture
Sept. 29, 2003 (Day 0)	Boulder Beach	M1	S00-S53, R00-R58	106	85	5	9	8.5
Oct. 2, 2003 (Day 3)	Boulder Beach	M2	S54-S99, R59-R99, V00,V17, V37-V99, W00-W99, H00-H42, H51-H75	308	84.1	4	9	2.9
Sept. 30, 2003 (Day 0)	Buckley's Cove	M1	V01-V16; V18-V36	30	88.8	8	0	0
Oct. 4, 2003 (Day 4)	Buckley's Cove	M2	K00-K24	24	88.9	6	0	0
Oct. 8, 2003 (Day 8)	Buckley's Cove	M3	K25-K99, H43-H50, H76-H92	93	88.8	5	2	2.2
Oct. 15, 2003 (Day 15)	Buckley's Cove	M4	H93-H98, I00-I66	72	91.1	4	0	0
Oct. 21, 2003 (Day 21)	Buckley's Cove	M5	I67-I83	16	99.6	4	0	0
Oct. 1, 2003 (Day 0)	Dockside	M1	L00-L42, F00-F59	101	88.8	5	2	2
Oct. 4, 2003 (Day 3)	Dockside	M2	G00-G08	8	89	5	0	0
Oct. 9, 2003 (Day 7)	Dockside	M3	G09-G16	7	91	3	0	0
				$\sum = 765$	$\bar{x} = 89.5$		$\sum = 22$	

Appendix 6

Table A9: The number of seines used to recapture VIalpha age-0 Greenland cod (*Gadus ogac*) for each sampling day at Boulder Beach, Hefferns Cove, and Otter Cove during the period of September 29 to October 28, 2003. Day 0 refers to the day juvenile cod were collected for tagging purposes.

Site	Number of Seines					
	September 29 (Day 0)	October 2 (Day 3)	October 7 (Day 8)	October 14 (Day 15)	October 21 (Day 22)	October 28 (Day 29)
Boulder Beach	11	12	2	3	3	2
Hefferns Cove	0	3	3	3	2	2
Otter Cove	0	3	3	3	2	3

Appendix 6 (cont.)

Table A10: The number of seines used to recapture VIalpha age-0 Greenland cod (*Gadus ogac*) for each sampling day at Buckley's Cove, Mistaken Cove, and Pipers Cove during the period of September 30 to October 21, 2003. Day 0 refers to the day juvenile cod were collected for tagging purposes.

Site	Number of Seines				
	September 30 (Day 0)	October 4 (Day 5)	October 8 (Day 9)	October 15 (Day 16)	October 21 (Day 22)
Buckley's Cove	13	6	9	3	4
Mistaken Cove	0	3	2	3	3
Pipers Cove	0	3	2	1	2

Appendix 6 (cont)

Table A11: The number of seines used to recapture VIalpha age-0 Greenland cod (*Gadus ogac*) for each sampling day at Dockside, Stairs Beach, and Whiterock during the period of October 1-16, 2003. Day 0 refers to the day juvenile cod were collected for tagging purposes.

Site	Number of Seines			
	October 1 (Day 0)	October 4 (Day 3)	October 9 (Day 8)	October 16 (Day 15)
Boulder Beach	11	12	2	3
Hefferns Cove	0	3	3	3
Otter Cove	0	3	3	3

Appendix 7

Table A12: Measurement error of 8 cunners (*T. adspersus*) across five independent observers using a measuring board marked in millimetres. Percent error was determined as the ratio of standard error to mean length. Data by S. Mayor, Department of Biology, Memorial University of Newfoundland.

Fish	Mean Length (mmSL)	Number of Observations	Standard Deviation (mmSL)	Standard Error (mmSL)	Percent Error (%)
A	44.2	5	0.45	0.20	0.45
B	84.0	5	0.71	0.32	0.38
C	91.4	5	1.95	0.87	0.95
D	45.4	5	0.89	0.40	0.88
E	40.6	5	0.55	0.25	0.60
F	78.2	5	1.10	0.49	0.63
G	45.4	5	0.89	0.40	0.88
H	48.8	5	0.84	0.37	0.77
Pooled	59.8	40	1.02	0.16	0.27